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Chapter 3

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Katarina E. Fussmann, Benjamin Rosenbaum, Ulrich Brose, Björn C. Rall

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In review in *Ecology and Evolution*

Chapter 4

Temperature adaptation of predator interference

Katarina E. Fussmann, Benjamin Rosenbaum, Ulrich Brose, Björn C. Rall

K.E.F., U.B. and B.C.R. designed the microcosm experiment. K.E.F. conducted the experiments. Statistical procedures on functional responses were carried out by B.R., B.C.R and K.E.F.. All authors contributed to the manuscript.

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Summary

Climate change is progressing fast causing losses in biodiversity to the extent that scientists believe the world to be on the brink of the sixth wave of mass extinction. While some global change drivers like pollution, nutrient enrichment or extended land-use on the expense of natural habitats may pose more obvious threats to ecosystems, even seemingly small changes in temperature as they are predicted for this century can have detrimental effects on populations and entire ecosystems. Temperature influences ecological processes through their underlying biological rates like metabolism, growth rate, carrying capacity and various feeding parameters, determining population stability and species interactions. However, the influence of temperature is not uniform, and unsynchronised changes in these rates can alter the strength of species interactions which are an important indicator of population stability.

While previous studies suggested an increase in predator-prey oscillations, this does not conform with experimental data, and the mechanistic understanding is still lacking. Therefore, I conducted time series experiments in a microbial predator-prey system with the ciliated predator *Tetrahymena pyriformis* preying on the bacteria *Pseudomonas fluorescens* along a temperature gradient combined with theoretical simulations based on a new global database for the temperature dependency of carrying capacity, half-saturation density, maximum feeding rate and metabolism (Chapter 2). Increasing predator-prey oscillations with warming as predicted by previous studies were only reported in 8.9 % of one million simulations and caused by a faster increase in maximum resource density with temperature than in foraging efficiency. In 91.1 % of simulations, predator-prey oscillations were stabilised with warming based on a faster increase in foraging efficiency with warming than in maximum resource density. Despite stabilising dynamics, in 73.6 % of simulations, predators went into extinction due to a faster increase in metabolism with temperature than in maximum feeding rate. This mismatch leads to predator starvation even under high prey abundances and stabile population dynamics, posing a challenge for conservation programs trying to preserve biodiversity in a changing world.

However, species have shown to adapt to changing environmental conditions on ecological time scales raising the question whether temperature adaptation of predators could provide a feasible way out of the extinction scenario. While only very few studies focus on predator adaptation, temperature adaptation of predator interference has not been documented

to date although it is a common pattern in ecological systems. Therefore, I conducted functional response experiments along an experimental temperature gradient within the microbial framework with predators adapted to a range of adaptation different temperatures to test for temperature adaptation of feeding parameters (Chapter 3) and predator interference (Chapter 4). My results show that the ciliated predator *Tetrahymena pyriformis* is able to increase activation energies for maximum feeding rate after an adaptation period of approximately 20 generations to higher temperatures compared to predators adapted to colder temperatures. Further, predators adapted to higher temperatures developed smaller body sizes, reducing their energetic demands potentially counteracting a mismatch between energy gain and energetic demand with rising temperatures. Predator interference increased with warming with the highest rates and shallowest increase with experimental temperature in warm-adapted predators, corroborating the assumptions of an improved energy budget in predators adapted to warmer temperatures. Due to higher levels of predator interference, maximum feeding rates were lowered in warm adapted predators, especially at low experimental temperatures which could have stabilising effects on predator-prey oscillations. Further, as a result of a stronger increase in attack rates and simultaneously a shallower decrease in handling times with increasing experimental temperature, half-saturation densities decrease for predators adapted to colder temperatures. The opposite is the case for warm-adapted predators. Increasing half-saturation densities with experimental temperature in warm-adapted predators potentially have an additional stabilising effect on predator-prey dynamics by controlling the energy flux together with carrying capacity.

My results suggest that the stabilising effect of temperature on predator-prey dynamics might be increased by temperature adaptation of predators. Further, a potential adaptation of feeding rates as well as metabolism, either through body size or potentially through physiological adaptation, might increase a predator's energy budget and prevent a mismatch between energy gain and energetic demand to prevent extinction. However, smaller body sizes can increase the vulnerability of a predator towards further, more sudden increases in temperature. In my thesis, I provide the mechanistic understanding for a reported trend towards food webs with smaller organisms and fewer links as well as findings that taxa adapted to tropical environments might be more vulnerable to short-term changes in temperature.

Part I.

General introduction

Chapter 1.

Introduction

Climate change

Climate change and its toll on biodiversity is ubiquitous across all realms of life (Thomas *et al.*, 2004; Duraiappah *et al.*, 2005; Botkin *et al.*, 2007) with the world potentially on the brink of a wave of mass extinction (Wake and Vredenburg, 2008; Barnosky *et al.*, 2011). Studies predict a decline in population abundances and biodiversity in terrestrial and aquatic systems with increasing temperatures (Thomas *et al.*, 2004; Alder *et al.*, 2007; Alkemade *et al.*, 2009; Hof *et al.*, 2011; Bellard *et al.*, 2012) that might be even greater than previously expected (Pereira *et al.*, 2010) wherever dispersal to more suitable habitats or persistence through phenotypic plasticity and evolutionary adaptation is not possible (Visser, 2008; Quintero and Wiens, 2013). Compared to global change stressors like draught, land-use change, or compartmentalisation of ecosystems, warming can have less obvious, but nonetheless severe, effects on biodiversity (Mayhew *et al.*, 2008). Scientists predict an increase in average surface temperature of 1.5° C over the time span of a century (IPCC, 2014). Although this might not sound dramatic, even small changes in temperature affect different biological rates and their delicate interplay (Rall *et al.*, 2012; Binzer *et al.*, 2012; Fussmann *et al.*, 2014) which can disturb population dynamics and scale up through entire food webs to large-scale impacts. Besides the decoupling effects of temperature on different biological rates itself, influencing species interactions, the adaptation of feeding can have additional consequences for interaction strengths and therefore ecosystem stability (Sentis *et al.*, 2014). In a meta-study investigating potential reasons for temperature induced extinctions, Cahill et al. (2012) found that the majority of studies suggested altered species interactions as an important cause for extinction (Gilman *et al.*, 2010; Urban *et al.*, 2012). This shift in interactions plays a vital role when understanding climate responses (Tylianakis *et al.*, 2008; Post, 2013) but unfortunately is hard to trace and even harder to prevent by protective strategies as the knowledge of the underlying mechanistics of these processes is still lacking.

Temperature effects are particularly challenging for species in freshwater systems since

microhabitats and refuges are scarce (Sommer *et al.*, 2012; Kratina *et al.*, 2012; Winder and Schindler, 2004). While in terrestrial systems species have the option to migrate to cooler microhabitats (Cowles and Bogert, 1944; Stevenson, 1985), species in marine systems have shown a poleward shift (IPCC, 2007) or migrate to greater depth to avoid high temperatures (Dulvy *et al.*, 2008). In freshwater systems, however, the capacity to avoid high temperatures is much more limited (Pereira *et al.*, 2010) due to geographically confined stream systems with limited depths. Without refuges or suitable habitats to migrate to, freshwater species have to rely on phenotypic plasticity or genetic adaptation to mitigate the effects of global warming (Berg *et al.*, 2010; Chevin *et al.*, 2010).

Metabolic theory of ecology

The Metabolic Theory of Ecology is a universal model describing temperature and body size dependence of biological rates (Brown *et al.*, 2004). This theorem holds for many rates determining population dynamics, such as growth rate, carrying capacity and mortality as well as population interactions such as predation and competition. Metabolism determines the transformation of nutrients into carbon sources and its allocation to life-sustaining biological processes. Therefore, it not only determines an organism's requirements to its environment but also the pace of all required processes. All processes underly the fundamental principles of biochemistry, namely enzyme kinetics (Enquist *et al.*, 1999; Gillooly *et al.*, 2001; Brown *et al.*, 2004). Resembling the Michaelis-Menten theory for enzyme kinetics, the Arrhenius equation including the Boltzmann factor can be used to describe the exponential increase of chemical reactions and, therefore, biological processes with temperature.

Arrhenius temperature and activation energies

To quantify the impact of temperature on different biological rates, I used the Arrhenius equation to calculate individual activation energies E_x. The Arrhenius equation was originally formed to describe chemical reactions (Schoolfield *et al.*, 1981; Van't Hoff, 1884; Arrhenius, 1889). It was implemented into biological studies with the argument that all biological processes depend on the underlying chemical and enzymatic reactions in their speed and temperature dependence (Gillooly *et al.*, 2001; Brown *et al.*, 2004; Savage *et al.*, 2004). Activation energies are calculated by transforming experimental temperatures into Arrhenius temperatures measured in Kelvin:

$$Arrhenius\ temperature = \frac{T_e - T_0}{kT_eT_0}\ , \tag{1.1}$$

where T_e is the absolute experimental temperature $[K]$, T_0 is the normalisation

temperature of the experiment $[K]$, and k is the Boltzmann constant $[eVK^{-1}]$. To obtain the slope of the relationship, which equals the activation energy E_x for a specific biological rate, we use the respective normalisation constant x_0 which is the intercept of the slope (Brown *et al.*, 2004) (Figure 1.1).

$$x = x_0 e^{E_x \frac{T_e - T_0}{kT_eT_0}} \tag{1.2}$$

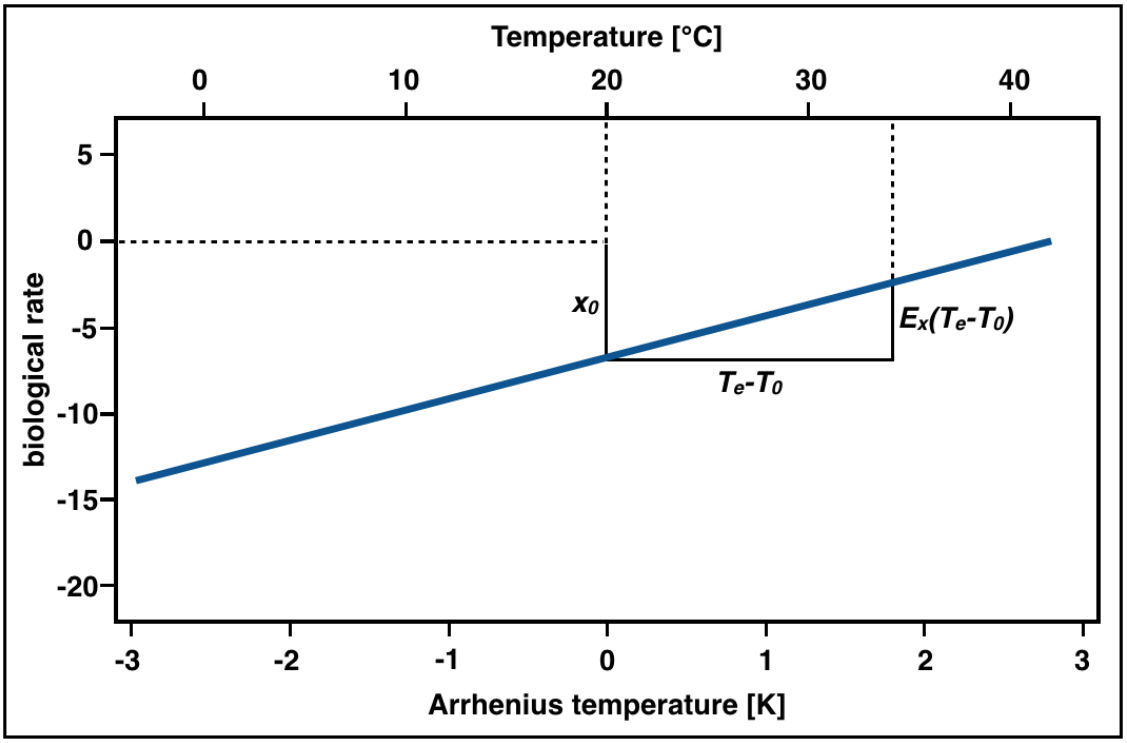

Figure 1.1 – The Arrhenius temperature $(T_e - T_0)/kT_eT_0)$ is plotted against the measured biological rate at the respective temperatures. We can obtain the normalisation constant x_0 from the intercept of the curve. The activation energy E_x for the temperature range $(T_e - T_0)$ is given by the slope of the relationship.

Further, this holds not only for experimental temperature but also the temperature of adaptation A_x (equation 1.3) and the interactive effect of experimental and adaptation temperature I_x (equation 1.4).

$$x = x_0 e^{E_x \frac{T_e - T_0}{kT_eT_0}} \; e^{A_x \frac{T_a - T_0}{kT_aT_0}} \tag{1.3}$$

$$x = x_0 \; e^{E_x \frac{(T_e - T_0)}{kT_e - T_0}} \; e^{A_x \frac{(T_a - T_0)}{kT_a - T_0}} \; e^{I_x \frac{(T_e - T_0)}{kT_e - T_0} \frac{(T_a - T_0)}{kT_a - T_0}} \tag{1.4}$$

This mechanistic model holds between 0 °C and 40 °C, the relevant temperature range for natural systems (Brown *et al.*, 2004; Irlich *et al.*, 2009). Activation energies are an important tool in climate change research to quantify and compare the impact of temperature on different biological rates, to understand the underlying consequences for populations and species interactions (Brown *et al.*, 2004; Savage *et al.*, 2004; Angilletta, 2006; Englund *et al.*, 2011; Vucic-Pestic *et al.*, 2011; Corkrey *et al.*, 2012; Rall *et al.*, 2012; Binzer *et al.*, 2016) and evolutionary processes (Gillooly *et al.*, 2005).

Population stability and interaction strengths

Population stability is often investigated in time-series experiments, recording the abundance of one or several populations at different time points within the experimental time frame (Figure 1.2). The monitoring of populations with the help of time series has been a valuable tool for conservational biologists over the last decades (Elton and Nicholson, 1942; Brand *et al.*, 1976; O'Donoghue *et al.*, 1997). In time series with a prey population as well as a predator population, population densities are hardly constant but oscillate around an equilibrium density, and the predator usually follows the prey oscillations with a phase-shift of 1/4 (Figure 1.2a). When prey abundances are high, predators respond numerically and grow to higher densities. The increased number of predators will cause prey abundances to dwindle. With the decreased supply in resources, predator abundances decline, releasing prey from predatory pressure causing prey abundances to rise again, followed by predator abundances, closing the circle. These oscillations can be mathematically described by their frequency, amplitude and the equilibrium density (Figure 1.2b). Frequency and amplitude of these oscillations are highly dependent on the interaction strength between prey and predator (May, 1972; de Ruiter *et al.*, 1995) described mathematically as the log ratio between prey densities with predators versus prey densities without predators (Berlow, 1999; Berlow *et al.*, 2004). Therefore, interaction strengths are on one side dependent on the abundance of prey without predators, determined by population growth rate of the prey population and the carrying capacity of the system, on the other side on the abundance of prey with predators present resulting from the maximum feeding rate and feeding efficiency of predators. An increase in feeding rates increases interaction strength and the amplitude of predator-prey oscillations, a reduction in feeding rates reduces interaction strengths and stabilises predator-prey oscillations.

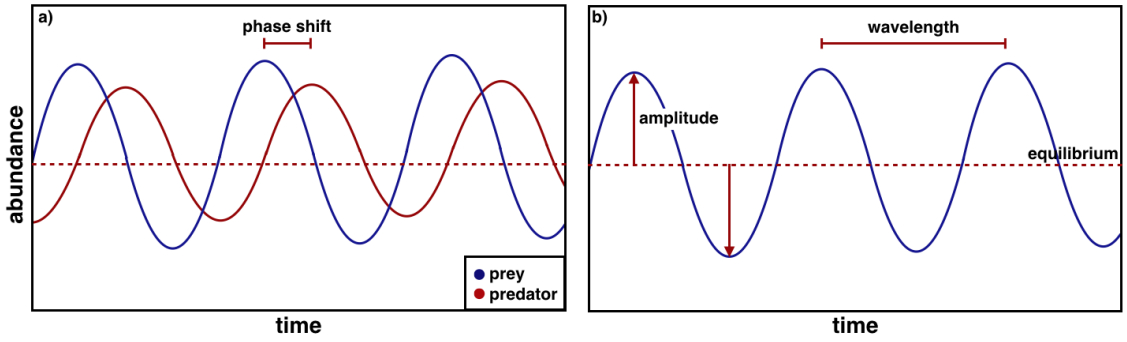

Figure 1.2 – **a)** Predator-prey oscillations are usually characterised by a phase shift of 1/4 with the predator population following the prey population in its oscillations. **b)** Population oscillations can be described by their amplitude, the amount the population deviates from its equilibrium density and the wavelength, the frequency of minima and maxima reoccurring over time.

Population dynamics under warming

Temperature alters different biological rates determining predator-prey interactions (Brown *et al.*, 2004) to various extents and not synchronous (Vucic-Pestic *et al.*, 2011). This affects interaction strengths and population stability (May, 1972; McCann, 2000; Brose *et al.*, 2006; Rall *et al.*, 2010). Following the metabolic theory of ecology, metabolism increases with warming (Hansen *et al.*, 1997; Gillooly *et al.*, 2001; Brown *et al.*, 2004; Savage *et al.*, 2004; Meehan, 2006; Ehnes *et al.*, 2011). This increase in metabolism increases the energetic demand of organisms and, therefore, reduces the carrying capacity of an ecosystem when resource availability is unaffected (Allen *et al.*, 2002; Brown *et al.*, 2004; Meehan, 2006; Delong and Hanson, 2011; Binzer *et al.*, 2012). To counteract increasing metabolic demands with warming, predators increase their feeding expressed by the half-saturation density and maximum feeding rate. In cases where feeding increases faster with temperature than the metabolic demands of the predator, warming leads to a numerical response, increasing predator abundance. This increases overall population top-down pressure and destabilises the feeding interaction (Vasseur and McCann, 2005). In populations with large amplitude cycles, even small disturbances can lead to the extinction of either prey, predator, or both (Rosenzweig, 1971; Vasseur and McCann, 2005). In cases, where metabolic demands increase faster with temperature than maximum feeding rates, predator abundances decrease, the top-down pressure is lowered, and population oscillations are predicted to stabilise (Vasseur and McCann, 2005). However, empirical data as well as theoretical predictions have not been coherent with these projections (Rall *et al.*, 2010; Binzer *et al.*, 2011). Therefore, I conducted time series experiments combined with a theoretical analysis of a new global database to bridge the gap between empirical evidence and mechanistic understanding in Chapter 2.

The functional response

The functional response is one of the oldest and most established tools to describe species interactions in the form of predator-prey relationships (Solomon, 1949). Species interactions play a fundamental role in understanding and quantifying interaction strengths and, therefore, predicting population dynamics determining ecosystem stability and biodiversity (Berlow *et al.*, 2009). In its simplest form, the functional response quantifies a predator's consumption directly proportional to prey density. This concept was independently developed by Lotka (1920; 1925) and Volterra (1928) and later added to Holling's framework as Type I functional response (Figure 1.3a, equation 1.5). Predator feeding F increases linearly with prey density without saturation. Without predators present, prey abundance increases exponentially. This allows prey to grow into irrelevant densities in the absence of predators, a flaw that was fixed in later models by introducing the carrying capacity K which sets an upper boundary to resource growth rates through resource availability (Watt, 1959; Holling, 1959*b*; Rosenzweig and MacArthur, 1963; Rosenzweig, 1971).

$$F = cN \tag{1.5}$$

N is the prey density changing over time t with the feeding rate determined by the attack coefficient c. The Lotka-Volterra model or Type I functional response most accurately describes the behaviour of filter feeders and certain web-building spiders (Holling, 1965).

Holling's predator-dependent Type II functional response (Figure 1.3b, d, equation 1.6) advances the basic model by replacing the solely encounter dependent predation rate with attack rate a and handling time h. With increasing prey density, feeding rates react more slowly to increasing prey densities until they reach a plateau where attack rates become negligible and maximum feeding rates f are restricted by handling time.

$$F = \frac{aN}{1 + ahN} \tag{1.6}$$

Attack rates describe the increase of the functional response at low prey densities. Search time and efficiency depend on the maximum distance between the predator and its prey at which an attack is pursued, the percentage of attacks that result in a successful kill, mobility and speed of predator and prey and the intrinsic motivation of the predator to sacrifice energetic resources in order to overcome the prey (Holling, 1959*b*, 1966; Koen-Alonso, 2007). Handling time is constant and independent of prey density and limits feeding at high prey densities. Furthermore, handling time describes the time predators dedicate to one prey individual, including the time used for hunting and overcoming the prey, the time needed for the actual feeding and, the time after feeding until another prey is approached,

including resting, digesting and possibly cleaning time (Holling, 1959*b*, 1966; Jeschke *et al.*, 2002; Koen-Alonso, 2007). The maximum feeding rate f is the inverse of minimum handling time at high prey densities when search time is negligible (Koen-Alonso, 2007).

The Type III (Figure 1.3c, equation 1.8) functional response describes a predator-prey interaction, where a certain number of prey cannot be affected by predators due to prey switching of the predator (Holling, 1959*a*; Murdoch, 1969), learning behaviour (Tinbergen, 1960; Holling, 1965; Murdoch, 1973) or by escaping into refuges (Murdoch, 1973). Therefore, attack coefficients b (equation 1.7) of the Type III functional response are prey-density dependent, describing the sigmoid shape of the functional response (equation 1.8).

$$a = bN \tag{1.7}$$

$$F = \frac{bN^2}{1 + bhN^2} \tag{1.8}$$

Compared to the Type II functional response, the Type III functional response has a stabilising effect on predator-prey interactions due to its sigmoid shape, increasing, for example, its robustness against enrichment (Rosenzweig, 1971). However, since this stabilising effect occurs only at low prey densities, energy flow to higher trophic levels is kept low (Rall *et al.*, 2008).

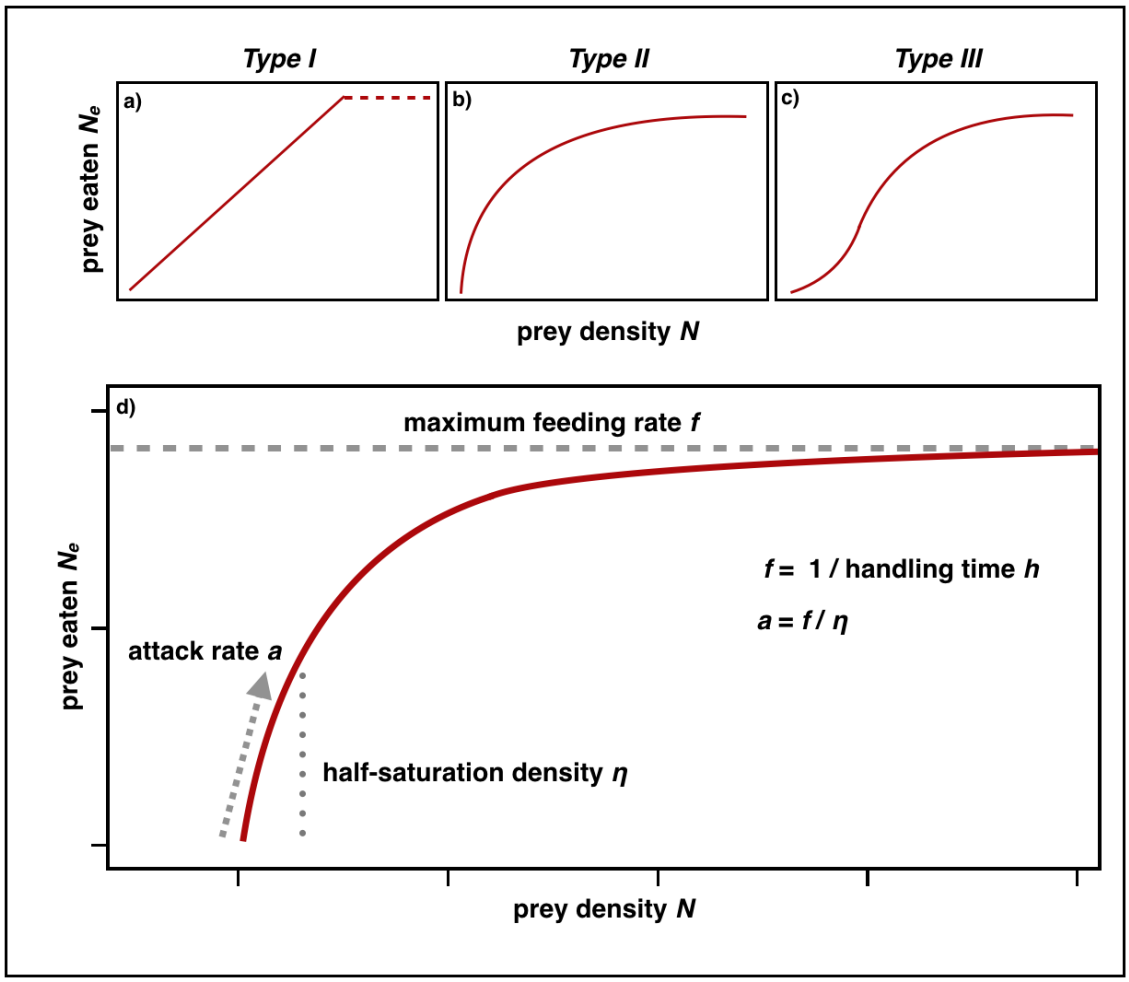

Figure 1.3 – Relationship between prey density and eaten prey according to the most common functional response types: a) Classic Holling Type I functional response as first described by Lotka 1920; 1925 and Volterra 1928. **b)** Saturating, hyperbolic Type II functional response c) The sigmoid Type III functional response is created through prey refuges, and therefore attack rates become prey density dependent. **d)** Exemplary Type II functional response curve: attack rate a determines the increase of feeding rate with prey density and characterises the functional response at low prey densities. At high prey densities, maximum feeding rate f is defined by handling time h. Illustrating maximum feeding rate f, attack rate a and half-saturation density η, the prey density at which half of the maximum feeding rate is reached.

Functional responses under warming

The biological parameters characterising functional responses are influenced by temperature (Vucic-Pestic *et al.*, 2011; Rall *et al.*, 2012; Lang *et al.*, 2012).

Attack rates increase exponentially with rising temperatures (Vucic-Pestic *et al.*, 2011) with an estimated activation energy of 0.42 eV (Rall *et al.*, 2012). Since warming increases activity and, for organisms in freshwater swimming speed, larger areas are searched leading to higher numbers of encounters (Dreisig, 1981; Honek, 1997; Kruse *et al.*, 2008; Dell *et al.*, 2014; Novich *et al.*, 2014). In the ciliated predator *Tetrahymena*, propulsion via cilia is directly related to cell temperature (Sleigh, 1956; Machemer, 1972; Riisgård and Larsen, 2009).

Handling times decrease exponentially with rising temperatures (Vucic-Pestic *et al.*, 2011) with an estimated activation energy of -0.30 eV (Rall 2012). Handling time, especially in unicellular organisms, strongly depends on digestion of prey (Jeschke *et al.*, 2002) which is mediated by temperature (Yee and Murray, 2004; Englund *et al.*, 2011; Dell *et al.*, 2014). This decrease in handling times simultaneously leads to an increase of maximum feeding rates with warming (Thompson, 1978; Vucic-Pestic *et al.*, 2011; Lang *et al.*, 2012; Sentis *et al.*, 2014).

Half-saturation densities are highly variable and can potentially increase with warming (Binzer *et al.*, 2012) when maximum feeding rates increase to a greater extent with temperature than attack rates (Figure 1.4a). Under the assumption that both, attack rate and maximum feeding rate increase simultaneously with increasing temperatures, half-saturation densities should not be affected by rising temperatures (Figure 1.4b). In cases where attack rates are affected more strongly by temperature than maximum feeding rates, half-saturation densities potentially decrease with increasing temperatures (Figure 1.4c). These warming-induced changes in functional response parameters are of particular importance given the global rise in temperature in terrestrial as well as freshwater systems and their importance for species interactions and population stability.

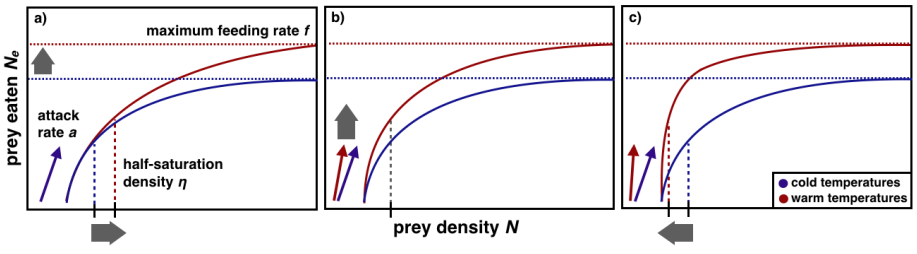

Figure 1.4 – **a)** Maximum feeding rate (dotted lines) increases with warming, while attack rate (arrow) is not affected. This leads to an increase in half-saturation density with increasing temperatures (dashed lines). **b)** Attack rate and maximum feeding rate increases with rising temperatures, resulting in a half-saturation density that is on average neutral. **c)** Maximum feeding rates increase with a strong increase in attack rates with rising temperatures resulting in decreasing half-saturation density.

Predator competition

Feeding interactions are not solely dependent on prey abundance and feeding efficiency of the predator. Predator abundance can play a crucial role determining interaction strengths of feeding interaction through predator interference which is common in natural systems (Watt, 1959; Hassell and Varley, 1969; Hassell and Rogers, 1972; Abrams and Ginzburg, 2000; Skalski and Gilliam, 2001; Vucetich *et al.*, 2002; Ginzburg and Jensen, 2008) and potentially an important driver of ecological and evolutionary dynamics (Gause, 1934).

Predator interference can be described by a wide range of mathematical models (Holling, 1959*b*; Hassell and Varley, 1969; Beddington, 1975; DeAngelis *et al.*, 1975; Hewett, 1980; Crowley and Martin, 1989; Skalski and Gilliam, 2001; Aljetlawi *et al.*, 2004; Vucic-Pestic *et al.*, 2010; Gonzalez-Suarez *et al.*, 2011). Two of the most established models are the Beddington-DeAngelis and Crowley-Martin interference functional response (Beddington, 1975; DeAngelis *et al.*, 1975; Crowley and Martin, 1989). Compared to ratio-dependent models (Hassell and Varley, 1969; Skalski and Gilliam, 2001), the Beddington-DeAngelis and Crowley-Martin model are based on a mechanistic approach following Holling's functional responses.

In the "distraction model" of the Beddington-DeAngelis functional response (equation 1.9), prey and other predators compete for a predator's attention affecting attack rates at low prey densities. At high prey abundances, the prey will be much more dominant than other predators. Therefore, predator interference is not affecting maximum feeding rates leading to a single asymptote (Figure 1.5a) (Beddington, 1975; DeAngelis *et al.*, 1975).

$$F = \frac{aN}{1 + ahN + cP} \tag{1.9}$$

In the "pre-emption model" of the Crowley-Martin functional response (equation 1.10), interference takes precedence over feeding and affects feeding rates at low and high prey abundances, leading to changes in attack rates and lower asymptotic feeding rates with increasing predator abundance (Figure 1.5b) (Crowley and Martin, 1989).

$$F = \frac{aN}{1 + ahN + cP + ahNcP} \tag{1.10}$$

The interference coefficient c can be mainly characterised by the number of encounters with other predators and the time spent on each interaction. Similar to attack rates, the number of encounters depends on the mobility of predators determining the relevant area and the potential number of encounters. Through time being taken away by interference, with multiple predators present, a portion of the usual area will not be searched for prey, reducing attack rates with a negative impact on feeding (DeAngelis *et al.*, 1975). The time spent on each interaction is, unlike the handling time of a functional response, dependent

on many different inner and outer circumstances determining hunger and physiological condition among others and, therefore, hard to predict.

Generally, predator interference alters feeding interactions, limiting the time for attacking prey (Beddington, 1975; Koen-Alonso, 2007). Interference usually has a negative impact on per-capita intake with increasing predator abundance (Watt, 1959; Hassell and Varley, 1969; Hassell and Rogers, 1972; Abrams and Ginzburg, 2000; Skalski and Gilliam, 2001), but single cases of positive effects on facilitation have also been documented (Royama, 1971; Abrams and Ginzburg, 2000). While higher predator interference and lower feeding interaction has the potential to stabilise population dynamics in protist systems (Terhorst *et al.*, 2010; Terhorst, 2011), generally stabilising predator-prey models (Hassell and May, 1973), population oscillations (Rall *et al.*, 2008) and entire food webs (Brose *et al.*, 2006), interference can also decrease fitness, lead to smaller predator biomasses and lower rates of survival (Arditi *et al.*, 2004; Kratina *et al.*, 2009).

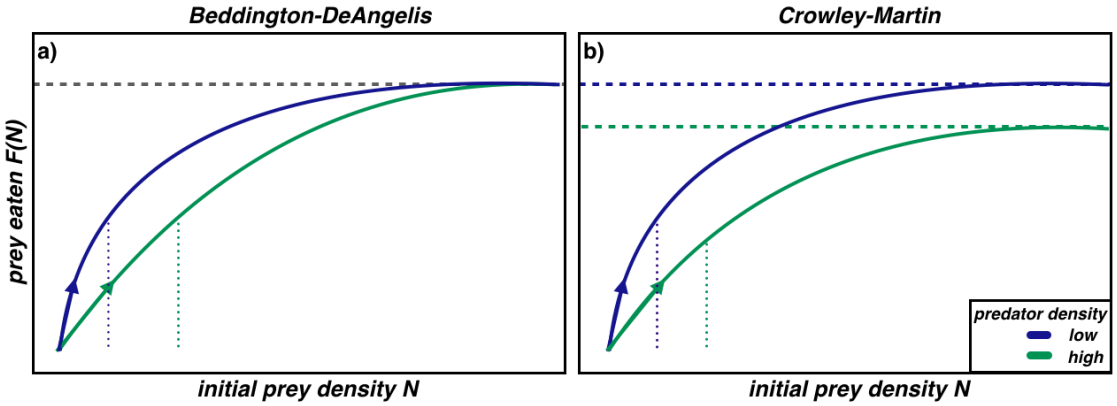

Figure 1.5 – **a)** Beddington-DeAngelis functional response describes decreasing attack rates (arrows) with increasing predator abundance, while maximum feeding rates (dashed lines) remain unaffected with a potentially high effect on half-saturation densities (dotted lines). **b)** Crowley-Martin functional response describes an effect of predator abundance on attack rates as well as maximum feeding rates.

Predator competition under warming

Predator interference can be divided into the encounter of other predators and the time spent on the interaction. The encounter rate resembles the attack rate of a predator-prey interaction as it is influenced by the swimming speed of predators and the area covered. With increasing temperature, movement increases leading to more encounters and increasing predator interference (Lang *et al.*, 2012). The time spent on an encounter with another predator resembles the handling time of a functional response. However, since it does not depend on the physiological process but rather on behaviour, the impact of temperature is difficult to estimate, and behaviour can buffer the impact of environmental change (Bogert, 1949; Huey *et al.*, 2003).

One predictor of interference behaviour can be the energy efficiency of a predator as speculated in Lang (2012) since time spent on predator interference is lost for attacking prey. In cases, where maximum feeding rates increase faster with warming than metabolic rates, leaving the predator with a very positive energy budget, predators are able to spend more time on each encounter with another predator. In cases where metabolism increases similarly fast with warming than maximum feeding rate, the energy gain becomes a limiting factor shifting a predator's priorities towards prey encounters and handling resulting in lower levels of predator interference and higher feeding rates. In extreme cases, however, where prey abundance is low and predators are under high energetic stress, predator interference possibly increases as a result of competition (Brown *et al.*, 2004; Savage *et al.*, 2004; Binzer *et al.*, 2012).

Increasing levels of predator interference with warming can potentially have stabilising effects on predator-prey interactions by lowering the maximum feeding rate and therefore the top-down pressure on the prey population. However, under the assumption of a possible energy limitation through a mismatch between metabolic rate and maximum feeding rate with increasing temperatures (Rall *et al.* 2010; Binzer *et al.* 2011; Chapter 2), predator interference could even enhance the extinction risk of predators due to starvation.

Adaptation to climate change

Natural selection is a powerful force (Endler, 1986) and the possibility that climate change triggers an evolutionary response is given (Holt, 1990; Lynch and Lande, 1993; Burger and Lynch, 1995; Merilä, 2012). While some studies argue, that this response might not be fast enough to keep up with climate change (Quintero and Wiens, 2013), other findings support the hypothesis that evolution can occur well within the timescales of ecological dynamics (Yoshida *et al.*, 2003; Fussmann *et al.*, 2007) and anthropogenic climate change (Huey and Kingsolver, 1993; Lenski and Bennett, 1993; Van Doorslaer *et al.*, 2009; Collins, 2011; Donelson *et al.*, 2011; Leuzinger and Thomas, 2011; Franks and Hoffmann, 2012; Lohbeck *et al.*, 2012; Dam, 2013). In studies where the selective response could keep pace with climate change, overall fitness was not affected dramatically (Huey and Bennett, 1987; Huey and Kingsolver, 1993; Lynch and Lande, 1993; Gomulkiewicz *et al.*, 1995; Chown *et al.*, 2010; Hoffmann, 2010; Hoffmann and Sgro, 2011).

When adapting to different environmental conditions, phenotypic plasticity and genetic adaptation are the dominant mechanisms (Chevin *et al.*, 2010). Phenotypic plasticity, the ability of an organism to vary its morphological, phenological, behavioural or physiological traits within the scope of its genotype is common and plays a significant role in buffering the gradual process of climate change (Chevin *et al.*, 2010; Donelson *et al.*, 2011; Huey *et al.*, 2012). Studies have documented phenotypic plasticity of heat tolerance in evolutionary history and high levels of phenotypic plasticity in heat resistance traits (Bahrndorff *et al.*, 2009; Fischer *et al.*, 2010; Sobek *et al.*, 2011). However, phenotypic plasticity comes at a cost that may limit population persistence (Chevin *et al.*, 2010). The extent to which phenotypic plasticity can buffer gradual changes in climate is affected by the size of a population and its genetic variation (Frankham, 1996; Johnson and Stinchcombe, 2007).

An increase of genetic variation through the evolution of new genotypes is mostly determined by the availability of preexisting genetic variation within a population and the strength of natural selection (Frankham, 1996; Johnson and Stinchcombe, 2007; Lohbeck *et al.*, 2012). Genetic adaptation via de-novo mutations is difficult since many small adaptations in different alleles are needed (Hoffmann *et al.*, 2015) but has been documented in phytoplankton populations (Schaum *et al.*, 2014). Evolutionary rates increase under warming due to an increased molecular clock (Gillooly *et al.*, 2005) allowing persistence under stronger environmental change (Chevin *et al.*, 2010). However, direct molecular observation of genetic temperature adaptation is difficult since the genetic underpinnings of most traits are still unknown (Mackay *et al.*, 2009; Anderson *et al.*, 2013).

In ecological research, disentangling the impact of plastic and genetic components is challenging (Gienapp *et al.*, 2008). Plastic response and genetic adaptation most likely operate at the same time (Merilä and Hendry, 2014). In fact, phenotypic changes potentially

can be transmitted between generations through mechanisms like epigenetic inheritance and can, therefore, have long-term carry-over effects influencing genetic variation, highlighting the importance of trans-generational studies (Jablonka and Raz, 2009; Donelson *et al.*, 2011; Schmitz and Ecker, 2012).

In natural environments, all species interact with other species through different pathways (Johnson and Stinchcombe, 2007). Species interactions and the many parameters they are characterised by have the potential to counter or exacerbate direct effects of climate change (Suttle *et al.*, 2007; Harley, 2011). Further, they are important drivers of evolutionary change (Murren *et al.*, 2014) and can increase thermal plasticity (Tseng and O'Connor, 2015). Regarding feeding interactions and the potential mismatch between energetic demand and energy gain that comes with warming, different adaptation strategies could arise. To decrease energetic demands, organisms can down-regulate their metabolism establishing a higher thermal tolerance (Krogh, 1916; Clarke, 1991; Addo-Bediako *et al.*, 2000). Corroborating these results, higher predator equilibrium densities with acclimation to higher temperatures have been documented (Sentis *et al.*, 2015). To increase energy gain, studies found increased feeding rates in warm acclimated predators to counteract increasing energetic demands (Sentis *et al.*, 2015). The implications of changed feeding parameters under warming for interaction strengths and, therefore, population stability are hard to predict. Especially behavioural responses and the influence of potential body size adaptation under warming, affecting all underlying parameters, can alter interaction strengths and cause non-linear deviations (Englund *et al.*, 2011; Rall *et al.*, 2012; Twomey *et al.*, 2012).

Body size adaptation

Body size is, both, heritable and phenotypically plastic (Garnett, 1981), and decreases with external temperature for many ectotherm organisms across different taxa (Atkinson, 1994; Atkinson and Sibly, 1997; Atkinson *et al.*, 2003; Angilletta Jr., 2009). Further, body size predictably influences many biological rates characterising organisms, populations and species interactions (Huxley, 1932; Brown *et al.*, 2004). Simultaneous changes in body size and body size related parameters can potentially compensate effects solely driven by physiological adaptation and alter eco-evolutionary dynamics (Yoshida *et al.*, 2007).

Many biological rates follow a non-linear 3/4 power-law scaling with body size which is in theory based on the fractal-like design of surfaces and networks in biological organisms and can be described by so-called allometric equations (Brown *et al.*, 2004; Savage *et al.*, 2004). However, scaling relationships of functional response parameters with body size can vary greatly (Rall *et al.*, 2012) since they are not only influenced by the size of the predator but the body size ratio between prey and predator.

In the context of global change, organisms have been found to adapt their body size to maximise the use of their resource (DeLong, 2014; Daufresne *et al.*, 2009; Yvon-Durocher *et al.*, 2011). Larger animals require more energy to function (Kleiber, 1932). Therefore, organisms reduce their body size to lower metabolic demands to survive and maintain reproduction (Margalef, 1954; Atkinson, 1996; Atkinson and Sibly, 1997; Woods, 1999). Further, smaller body size can increase evolutionary rates through faster cell division cycles and generation times (Stearns, 1976; Atkinson, 1994). On the flip side, organisms that have become too small can potentially get out-competed by better-adapted competitors. Generally, it has been documented, that warming favours smaller predators (Daufresne *et al.*, 2009; Yvon-Durocher *et al.*, 2011; West and Post, 2016) leading to food webs with smaller species (Petchey *et al.*, 2008; Petchey and Belgrano, 2010).

On the side of energetic demand, body size influences metabolic rates (Fenchel and Finlay, 1983) with a scaling exponent of 0.75 (Brody and Lardy, 1945; Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984; Enquist *et al.*, 1999; West *et al.*, 2000; Savage *et al.*, 2004; DeLong and Hanson, 2009; Schmitz and Ecker, 2012; Schneider *et al.*, 2012). While some studies suggest a slightly lower scaling coefficient (Ehnes *et al.*, 2011), studies in unicellular organisms propose a scaling coefficient of 1.0 (Okie *et al.*, 2016). Further, due to higher resting metabolism through constant swimming or floating activity Glazier (2006) suggests a scaling coefficient of 1.0 also for aquatic organisms. Reduced metabolic rates potentially lead to higher growth rates and higher carrying capacities.

On the side of energy gain through feeding interactions, the different functional response parameters are affected by body size. Attack rates are composed of various processes and can, therefore, vary with body size. Encounter rates and search radius decrease with

decreasing body size, due to slower movement speed in smaller organisms (Peters, 1983; McGill and Mittelbach, 2006). Therefore, smaller body size has a negative effect on attack rates (DeLong, 2014), possibly following a hump-shaped relationship (Rall *et al.*, 2012). Lower predator body size in relation to prey size leads to higher handling times with an allometric scaling of 0.66 to 1 (Rall *et al.*, 2012; DeLong, 2014). Hence, maximum feeding rates decrease with decreasing predator body size. Being influenced by both, attack rates and handling times, half-saturation densities can be affected by body size through one of the variables (Yoshida *et al.*, 2003) or can be independent of body size in cases where body size effects on attack rate and handling time become redundant (Hansen *et al.*, 1997). While some studies reported no effect of predator body size on predator interference (DeLong, 2014), other studies documented weaker interference in smaller predators (Leonardsson, 1991; Wissinger and McGrady, 1993; Lang *et al.*, 2012). Since all rates react differently to changing body size, body size adaptation has the potential to alter feeding interactions. Food web studies, basing predictions of interaction strengths on body size measurements (Brose, 2010) highlight the importance of body size for systematic effects in predator-prey interactions (Vucic-Pestic *et al.*, 2010; Rall *et al.*, 2012).

While temperature effects on different biological rates and their delicate interplay driving predator-prey interactions are not fully understood yet (Vucic-Pestic *et al.*, 2010; Rall *et al.*, 2012), we have an even more limited understanding of the effects of temperature adaptation of these rates (Sentis *et al.*, 2015). Since adaptations can potentially take place on the basis of physiological, behavioural as well as body size adaptation with effects that can increase or inhibit each other (Yoshida *et al.*, 2007), the effects on predator-prey interactions are hard to anticipate.

Microbial toolbox

Box and Draper, 1987, p74: *"For such a model there is no need to ask the question "Is the model true?". If "truth" is to be the "whole truth" the answer must be "No". Remember that all models are wrong; the practical question is how wrong do they have to be to not be useful."*

In order to document predator-prey time series and conduct adaptation experiments within a feasible time frame for my PhD, I decided to use a novel model system using bacteria as prey and ciliated protozoa as predators. Compared to other taxa, protozoa are surprisingly complex and include many different families with various characteristics, mainly grouped together because of their size. Just like different species in terrestrial ecosystems fill different niches and provide various ecosystem functions, protozoan species coexist in a complex community shaped by feeding interactions, competition, mutualism, facilitation, parasitism and many other common interaction patterns (Anderson and Druger, 1997; Montagnes *et al.*, 2012).

Historically, microorganisms were often disregarded as ecological model organisms because of a lack of suitable methodology and doubts about the applicability of observed patterns to larger scales. One of the first significant ecological studies using protozoans in microcosms to investigate species interactions was Gause's "Experimental analysis of Volterra's mathematical theory of the struggle for existence" (1934) followed by competition studies by Vandermeer (1969) and extensive studies on species' competition by Luckinbill (1973; 1974; 1979). Further, investigation of metabolism and energy efficiency in response to temperature and body size in protozoans have made a valuable contribution to understanding the impacts of global warming on population dynamics, not only in the microbial world (Fenchel, 1967, 1969; Laybourn, 1975; Laybourn and Finlay, 1976). Today, microcosms have become useful tools for exploring ecological and evolutionary processes (Krebs, 1975; Jessup *et al.*, 2004; Holyoak and Lawler, 2005; Montagnes *et al.*, 2012; Altermatt *et al.*, 2015) with groundbreaking results (Blackburn, 2010).

Microcosm experiments have many advantages over mesocosm, macrocosm, and field experiments. The organisms and ultimately the entire experimental setup do not require much space or funds and even complex temperature experiments with a full factorial design can be conducted in a single room with several thermostatic cabinets. In those cabinets, conditions like temperature, humidity, resource levels, light exposure and other factors can be easily controlled and monitored. Short generation times enable the study of adaptation processes in feasible time frames. Protozoans quickly respond to environmental

change, are easy to manipulate and are genetically and physiologically highly diverse in their response to stressors (Jiang and Morin, 2004; Montagnes *et al.*, 2012; Plebani *et al.*, 2015). The trophic complexity of protozoans allows the assembly of compound model systems to explore population oscillations and growth, predator-prey dynamics, competitive interactions and even entire communities and ecosystems in different scenarios under highly controlled conditions (Petchey *et al.*, 1999; Altermatt *et al.*, 2015). With the help of high-throughput cell counting techniques, species abundances can be easily obtained in big sample sizes and high numbers of replication.

Model organisms

In my microcosm experiments I used the bacterium *Pseuodmonas fluorescens* (Figure 1.6a) as prey and the ciliated protozoan predator *Tetrahymena pyriformis* (Figure 1.6b) in an aquatic environment.

Pseudomonas fluorescens is a gram-negativ, obligat aerob, rod-shaped, potentially pathogenic bacterium mostly found in soil with an average cell length of 1.5 - 2.0 μm and an average cell width of 0.5 - 0.6 μm (Rhodes 1959, Figure 1.6a). Certain biocontrol strains are known to protect plant roots from pathogens and itself from grazing through protists by producing a multitude of extracellular compounds, such as the antibiotics 2,4-diacetylphloroglucinol, pyoluteorin, and pyrrolnitrin, an extracellular protease, and hydrogen cyanide (Haas *et al.*, 2002; Weller *et al.*, 2007). The strain CHA19 which I used here, however, is a $\delta gacS$ mutant, not producing any of these metabolites (Zuber *et al.*, 2003), since they can be moderately toxic for *Tetrahymena* and, therefore, may influence predator-prey dynamics (Schlimme *et al.*, 1999). Further, the ability to form biofilms is inhibited in CHA19 (Zuber *et al.*, 2003) leaving the bacteria to float in the media with the help of multiple flagella as prey for the ciliated predator *Tetrahymena*. To enable accurate measurements of population abundances in time series as well as functional response experiments, the *Pseudomonas* strain CHA19 was transformed using miniTN7 transposons to introduce a GFP (Green Fluorescent Protein) marker (Lambertsen *et al.*, 2004). As a result, when excited at 488 nm, the bacteria will emit a green fluorescent signal at 508 nm which can be detected in flow cytometers or plate readers, generally producing more accurate results than measurements of optical density.

Tetrahymena pyriformis is a ciliated protozoan in the family of Hymenostomata and ubiquitous in aquatic freshwater systems and soil (Figure 1.6b). They are most common in saprobial waters with high densities of bacteria (Foissner, 1994) which form their main food source (Groupe *et al.*, 1955; Curds and Vandyke, 1966; Rasmussen, 1976; Fenchel, 1980; Swift *et al.*, 1982; Luna-Pabello *et al.*, 1990; Foissner, 1994). The pear-shaped unicellular

organism is usually around 40 - 60 μm long and 20 - 30 μm wide. They are characterised by their rows of around 7 μm long cilia (Winet, 1976) which make them active swimmers hunting for bacteria. One individual is able to filter approximately $1x10^{-6}$ ml to $1x10^{-5}$ ml per hour (Lavin *et al.*, 1990) and absorb food particles over the undulating membrane via phagocytosis into the cell. The feeding apparatus is relatively small and located at the narrower end of the cell. Size and shape of the filtering apparatus results in a size preference for prey and chemosensory attraction or repulsion combined with high swimming activity creates a "hunting behaviour" for suitable prey (Fenchel and Blackburn, 1999). Different species of the *Tetrahymena* genus are hard to distinguish and they are therefore rarely used as an indicator organism in ecosystem surveys. However, particularly the species *Tetrahymena pyriformis* and *Tetrahymena thermophila* have become popular model organisms in a vast variety of studies in different biological fields. In my studies, compared to other ciliated protozoan model organisms like *Paramecium* or *Didinium*, *Tetrahymena* had the advantage that it can be grown axenically, meaning, without any other organisms present (Curds and Cockburn, 1968). Therefore, it allowed the control of the entire bacterial community in experimental treatments without unaccounted contaminations.

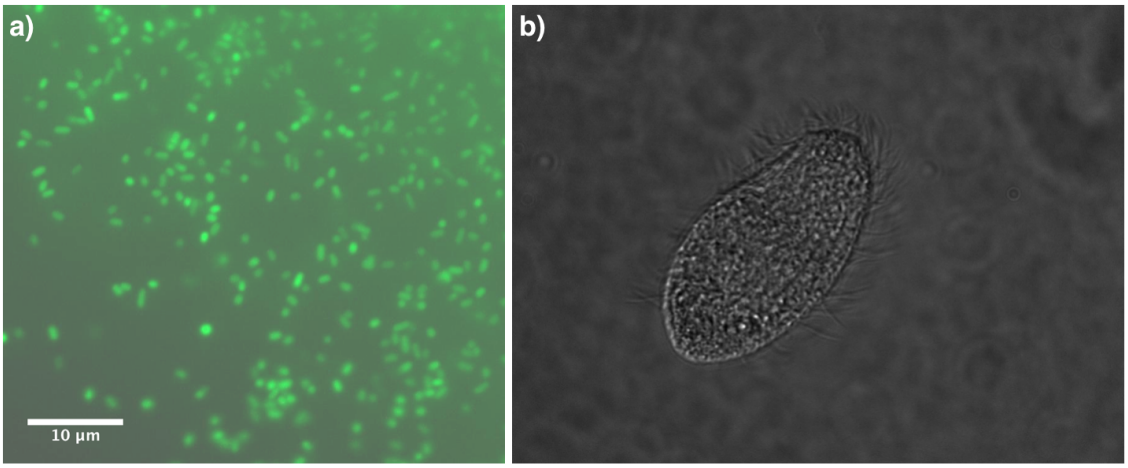

Figure 1.6 – **a)** Microscopic picture of the fluorescent marked bacterium *Pseudomonas fluorescens* CHA19-gfp in 100x magnification, bar shows 10 μm for comparison. **b)** Microscopic picture of the ciliated protozoan *Tetrahymena pyriformis* in 100x magnification.

Experimental setup

In Chapter 2, I conducted time series experiments at 15° C, 20° C, 25° C and 30° C with four replicates per temperature in thermostatic cabinets with 250 ml glass beakers as one experimental treatment (Figure 1.7). This temperature range reflects the realistic temperature range in temperate aquatic systems, both, in presence and absence of extreme temperature events (Seifert *et al.*, 2015). Every 24 hours, samples were drawn to monitor predator and prey abundances. Due to short generation times, several oscillations of the predator-prey systems were monitored in the relatively short time span of six weeks, highlighting one of the key advantages of microcosm experiments.

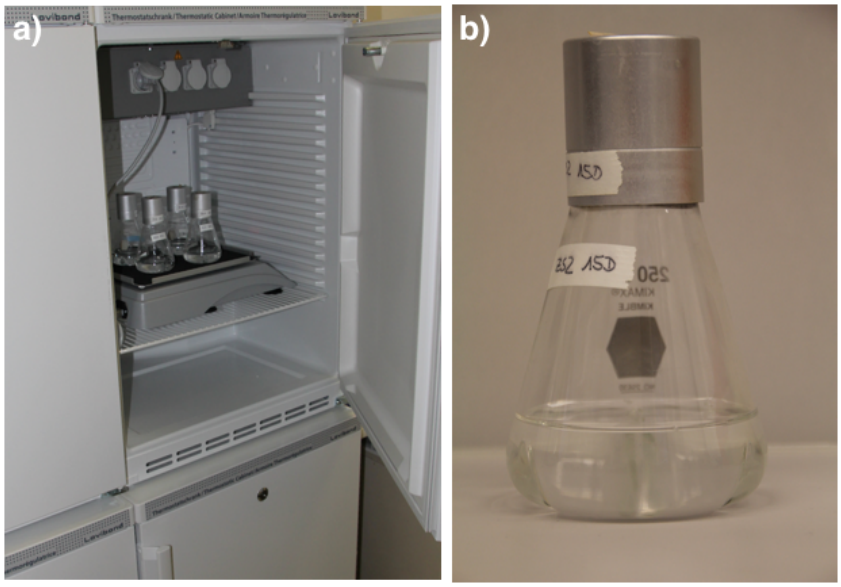

Figure 1.7 – Experimental setup of time-series experiments a) Experiments were run in thermostatic cabinets 4 different temperatures and 4 replicates per temperature. **b)** 250 ml Erlenmeyer borosilicat glass flasks closed with aluminium caps with bottom baffles to increase turbulence and promote gas exchange.

To explore the effect of temperature on feeding rates in Chapter 3 and Chapter 4, I conducted different functional response experiments with *Tetrahymena pyriformis* and *Pseudomonas fluorescens* in 96-well plates (Figure 1.8) at 15° C, 20° C and 25° C. This setup with eleven columns allowed for eleven different initial prey densities plus one additional control treatment containing only predators. With eight rows per 96-well plate, six rows were treated as replicates and two rows of control treatments containing no predatory ciliates and two media blanks. The GFP signal emitted by the bacteria was measured in a plate reader and matched to bacterial counts after establishing a regression

by directly monitoring bacterial counts in the flow cytometer. Most empirical studies of functional responses don't vary both prey and predator densities for logistical reasons (Kratina *et al.*, 2009), highlighting one further advantage of using microbial microcosms. Here, not only prey and predator densities are varied but also experimental temperature as well as adaptation temperature.

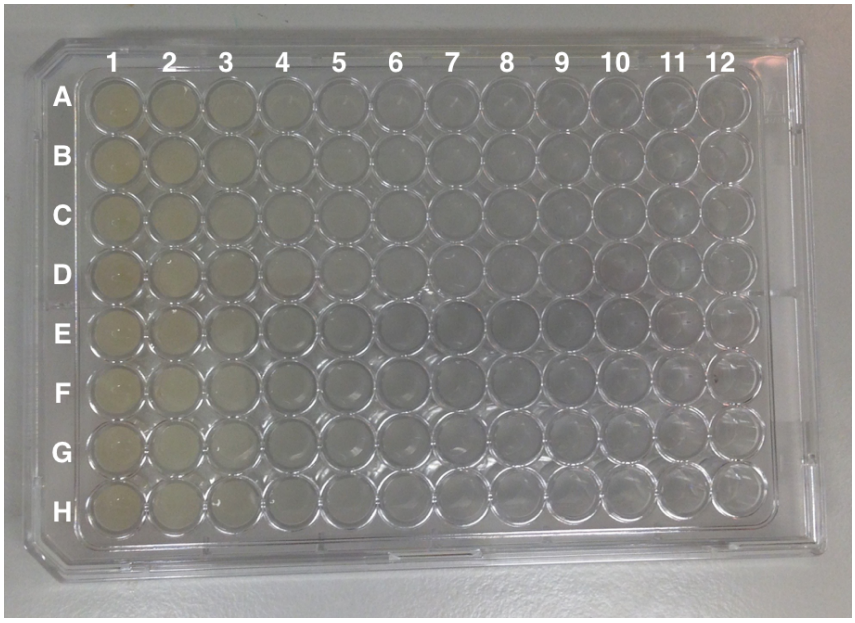

Figure 1.8 – **Experimental setup of functional response experiments** 96-well plate containing a dilution series of the bacterial prey *Pseudomonas fluorescens* CHA19-gfp from left to right (1-11), with the last column (12) as blank treatment. Rows A-F are identical functional response treatments, containing the predatory ciliate *Tetrahymena pyriformis*. Rows G and H are control treatments containing only the different initial densities of the bacterial prey.

Bayesian Statistics

For the analysis of my extensive functional response datasets in Chapter 3 and Chapter 4, I have chosen the Bayesian statistics approach due to its accuracy and reliability, especially when dealing with large datasets and complex ordinary differential equation models.

The original Bayes' theorem, named after Reverend Thomas Bayes (1701/1702 - 1761) is based on formulating probability distributions $p(A|B)$. It describes the probability of a hypothesis A based on an observation B through inverse probability $p(B|A)$ (Eddy, 2004). Although Bayes' theorem was developed in the 18th century, it was extremely hard to implement. The mathematical solution of Bayes' theorem (except for very simplified examples) requires integration over uncertain parameters without an analytical solution and therefore requires numerical integration (e.g. Markov-Chain Monte-Carlo) which is not feasible without modern computers (Eddy, 2004; Stevens, 2009; Palamara *et al.*, 2014).

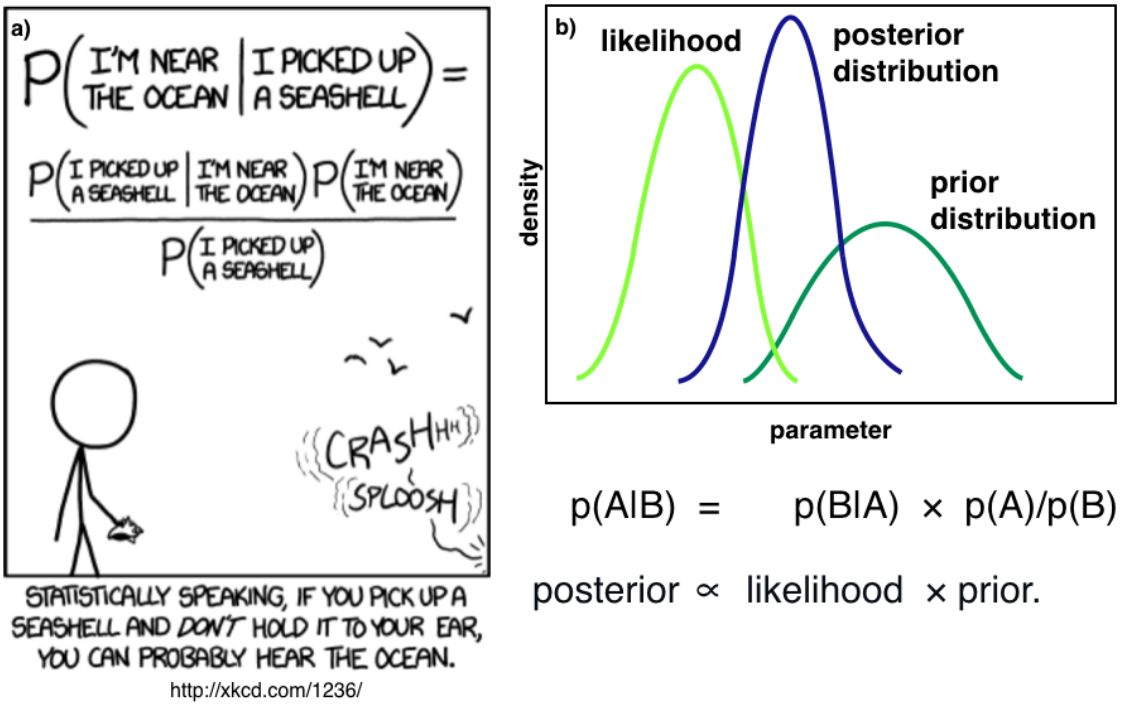

Figure 1.9 – **a)** Bayesian statistics explained by an illustration of xkcd webcomics (http://xkcd.com/1236/) **b)** Likelyhood and prior distribution leading to the posterior distribution as a probability distribution of the parameter of interest.

Empirical data drawn from experiments, form the likelihood function $p(B|A)$, the probability of picking up a seashell when being near the ocean, which is formulated as the probability of observed data B, all times a seashell has been picked up, under the condition A, of being near the ocean, and is one of two sources of information when analysing a parameter with Bayesian statistics (Figure 1.9a). The second source is the

prior distribution $p(A)/p(B)$ which can be based on assumptions, hypotheses or data from previous studies. Here it is the probability of being near the ocean, with or without picking up a seashell, $p(A)$, divided by $p(B)$, the probability of picking up a seashell, independent of the location. Since these priors influence the result of the analysis, uninformative priors in the form of flat distributions can be fed into the model. The end result, the probability distribution $p(A|B)$, the probability of being near the ocean when picking up a seashell and, therefore, hearing the sound of the waves without lifting the seashell to one's ear, is based on the information of the empirical data and the prior information (Stevens, 2009). When it comes to reporting results, the classic frequentist approach outputs one estimate per parameter together with a corresponding p-value. Bayesian statistics on the other hand report a distribution of the parameters, from which the mean can be drawn as the most probable value of the parameter, while the distribution itself contains additional information about the parameter such as variance or quantiles (Korner-Nievergelt *et al.*, 2015; Hector, 2015). 95 % credible intervals provide comparable information as F- and t-test, additional to the advantage that they are described on the same scale as the parameter making it easier to compare results of previous studies. Parameters of other studies that fall within the distribution are consistent with the data and are therefore supported by the hypothesis of the model. Since credible intervals are easier to reproduce than p-values, they provide a greater use for additional test and meta-analyses (Hector, 2015).

Research focus and questions

Anthropogenic climate change is progressing fast, threatening ecosystems worldwide (Cook *et al.*, 2013). Especially, increasing temperatures and their effect on biological rates determining species interactions is a complex field requiring in depth mechanistic understanding. Interaction strengths of predator-prey interactions are an important indicator of population dynamics and food web stability (McCann *et al.*, 1998; Rooney *et al.*, 2006; Berlow *et al.*, 2009; O'Gorman and Emmerson, 2009). While some studies suggest a destabilising effect of warming on predator and prey populations (Vasseur and McCann, 2005), other studies predict the opposite outcome with a stabilising effect on populations (Petchey *et al.*, 1999; Rall *et al.*, 2010), raising the question addressed in Chapter 2:

How does temperature affect population stability in predator-prey systems and what are the underlying mechanisms?

While potentially destabilising effects on population dynamics can trigger the extinction of either prey, predator, or both, by periodically lowering population densities and increasing vulnerability to other stressors, even under stabilising conditions, predators can be prone to extinction. A mismatch in the increase of metabolic cost and feeding efficiency with warming can potentially lead to predator starvation even under high prey abundances, leading to my second research question addressed in Chapter 3:

Do predators exposed to higher temperatures over several generations adapt to avoid a possible mismatch leading to extinction?

Further, predator interaction is not only a common phenomenon in natural systems, but can have severe effects on predator-prey interactions (Lang 2012). Therefore, predator interference can have significant impacts on population stability and needs to be considered when assessing climate change scenarios, leading to my third research question addressed in Chapter 4:

What is the effect of predator interference under increasing temperatures and how does temperature adaptation of interference affect predator-prey interactions?

In the following chapters addressing the stated questions, I aim to widen the mechanistic understanding of the impact of experimental temperature on population stability within predator-prey systems. Further, I want to highlight the impact of possible temperature adaptation of predators on feeding interactions to gain important insights into potential consequences of climate warming on population stability.

Part II.

Research chapters

Chapter 2.

Ecological stability in response to warming

Katarina E. Fussmann, Florian Schwarzmüller, Ulrich Brose, Alexandre Jousset, Björn C. Rall

Abstract

That species' biological rates including metabolism, growth and feeding scale with temperature is well established from warming experiments (Brown *et al.*, 2004). The interactive influence of these changes on population dynamics, however, remains uncertain. As a result, uncertainty about ecological stability in response under warming remains correspondingly high. In previous studies, severe consumer extinction waves in warmed microcosms (Petchey *et al.*, 1999) were explained in terms of warming-induced destabilisation of population oscillations (Vasseur and McCann, 2005).

Here, we show that warming stabilises predator-prey dynamics at the risk of predator extinction. Our results are based on meta-analyses of a global database of temperature effects on metabolic and feeding rates and maximum population size that includes species of different phylogenetic groups and ecosystem types. To unravel population-level consequences we parameterised a bioenergetic predator-prey model (Otto *et al.*, 2007) and simulated warming effects within ecological, non-evolutionary timescales.

In contrast to previous studies (Vasseur and McCann, 2005), we find that warming stabilised population oscillations up to a threshold temperature, which is true for most of the possible parameter combinations. Beyond the threshold level, warming caused predator extinction due to starvation. Predictions were tested in a microbial predator-prey system. Together, our results indicate a major change in how we expect climate change to alter natural ecosystems: warming should increase population stability while undermining species diversity.

Letter

Ongoing global warming is documented in different ecosystems worldwide (Parmesan, 2006; Solomon, 2007). Such global warming can lower abundances and lead to extinction, for example, due to habitat loss (Parmesan and Yohe, 2003; Thomas *et al.*, 2004; Parmesan, 2006; Thomas *et al.*, 2006). However, specific predictions of consequences for global ecosystems and species are still vague, because warming simultaneously affects many levels of ecological organisation. This includes simultaneous changes of multiple biological and biochemical rates with temperature (Vasseur and McCann, 2005; Rall *et al.*, 2008; Dell *et al.*, 2011): increased individual metabolic rate (Brown *et al.*, 2004) and intrinsic population growth (Savage *et al.*, 2004), as well as modified feeding parameters(maximum feeding and half-saturation density) of predator-prey interactions (Thomas *et al.*, 2006; Rall *et al.*, 2008; Englund *et al.*, 2011; Rall *et al.*, 2012) Figure 2.1a.

Traditionally, severe consumer extinction waves in warmed microcosms (Petchey *et al.*, 1999) were explained by increased metabolic and feeding rates that destabilise population dynamics by causing stronger oscillations (Vasseur and McCann, 2005). However, the lack of systematic empirical data and their integration with generalised models hampered an understanding of their interactive influence on population dynamics and species survival. Hence, predictions of warming effects on ecosystems and their stability remained highly uncertain. To overcome these limitations, we analysed a new global database and addressed how warming affects metabolic and feeding rates as well as maximum population size across species of different phylogenetic groups and ecosystem types.

Subsequently, we used these empirical physio-ecological scaling relationships and parameterised a bioenergetic model to predict warming effects on population stability and species' survival probabilities. We tested these predictions in a microbial microcosm experiment across a temperature gradient. Together, these integrated analyses provide a generalised understanding of how warming affects natural communities.

Temperature dependencies of biological rates (x) are commonly described by the Arrhenius equation (see Figure 2.1b with metabolic rates as an example):

$$x_c = x_0 \, e^{E_x \frac{T - T_0}{kTT_0}} \,, \tag{2.1}$$

where x_0 is a rate- and mass-dependent normalisation constant, E_x (eV) is the rate's activation energy, T is the absolute temperature of the system (K), k (eV K^{-1}) is Boltzmann's constant and T_0 (K) the normalisation temperature (here: 20° C = 293.15 K).

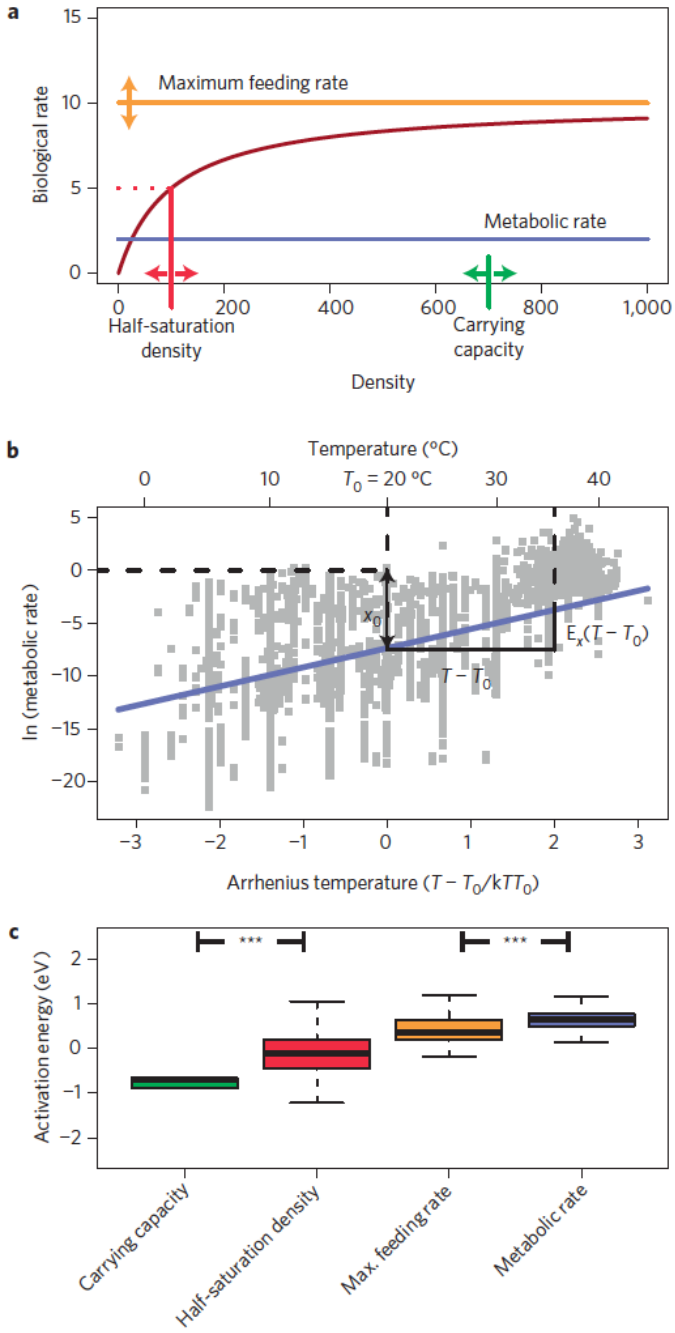

Figure 2.1 – Empirical warming effects on biological rates. **a**, Conceptual illustration of how temperature affects the parameters maximum feeding, half-saturation density (foraging inefficiency), carrying capacity (maximum prey density) and metabolic rate. The brown line shows the realised feeding rate. The vertical part of the red line shows the half-saturation density and the horizontal dashed part illustrates that at this prey density the half-maximum feeding rate is realised. **b**, Temperature scaling of metabolic rates as an illustration of activation energies (E_x) in Arrhenius equations. **c**, E_x for carrying capacity (mean= -0.77; s.d.=0.36), half-saturation density (mean= -0.12; s.d.=0.53), maximum feeding rate (mean=0.47; s.d.=0.44) and metabolic rate (mean=0.64; s.d.=0.29) in our empirical databases. Stars denote significant differences (***, $p < 0.001$) between pairs of rates as determined by F-tests (metabolic rate versus maximum feeding; carrying capacity versus half-saturation density).

Using a global database, we analysed activation energies for metabolic rates, carrying capacities (maximum density of the prey), maximum feeding rates and half-saturation densities (prey density at which half of the maximum feeding rate is realised, see Figure 2.1a, thus expressing the predator's foraging inefficiency), which are parameters of a bioenergetic population model of previous studies (Otto *et al.*, 2007; Boit *et al.*, 2012; Schneider *et al.*, 2012). Values for the intrinsic growth rate of resource populations were 0.84 eV for multicellular organisms with non-overlapping generations (Savage *et al.*, 2004). In our analyses, activation energies of the carrying capacity are generally negative, whereas activation energies of the half-saturation density are close to zero (Figure 2.1c). This significant difference suggests that predators cannot increase their foraging efficiency to cope with scarcer prey in warmer systems. Moreover, maximum feeding increases significantly less with warming than metabolic rate (lower activation energies, (Figure 2.1c), which implies that predators in warmer ecosystems suffer from increased energy loss owing to metabolism whereas their maximum energy intake cannot increase similarly. Both significant differences (as indicated in Figure 2.1c) suggest a reduced energy supply for predators in a warmed world.

To investigate the interplay of these warming effects with population dynamics, we used the average activation energies and their standard deviations to parameterise a bioenergetic model (Yodzis and Innes 1992; Brose *et al.* 2006; Binzer *et al.* 2012, Methods). We also implemented published data for the temperature dependency of resource population growth (Savage *et al.*, 2004). Our initial model simulations were based on the average activation energies (see legend of Figures 2.1a, b, c, and Appendix Table 1) to predict dynamics along a temperature gradient (0° - 40° C). We found predator extinctions at low temperatures (<11° C) due to unstable population dynamics. Predators and prey persisted along a temperature range between 11° C and 27.5° C, whereas above 27.5° C predators became extinct owing to energy limitations (Figure 2.2a). Although these temperature thresholds remain specific for the average activation energies, our analyses indicate the general pattern that within the persistence range, increasing temperatures cause decreasing amplitudes of population oscillations - thus stabilising predator-prey systems from limit cycle (Fig. 2.2b) into equilibrium dynamics (Figure 2.2d). Although warming increases per-unit biomass flux rates, the much stronger metabolic acceleration (Figure 2.1c) leads to lower consumer biomass densities and eventually reduces population-level fluxes. Furthermore, a decline in prey densities (carrying capacities) that is stronger than the decrease in half-saturation densities (Figure 2.1c) and the associated increase in foraging efficiencies also lowers the population-level fluxes. Consequently, these two main effects cause dampened oscillations due to lower top-down pressure and higher risk of predator starvation as a consequence of lower bottom-up energy supply (Rip and McCann, 2011). Thus, warming reduces

population energy fluxes and leads to dynamics that are similar to an inverse paradox of enrichment (Rosenzweig, 1971).

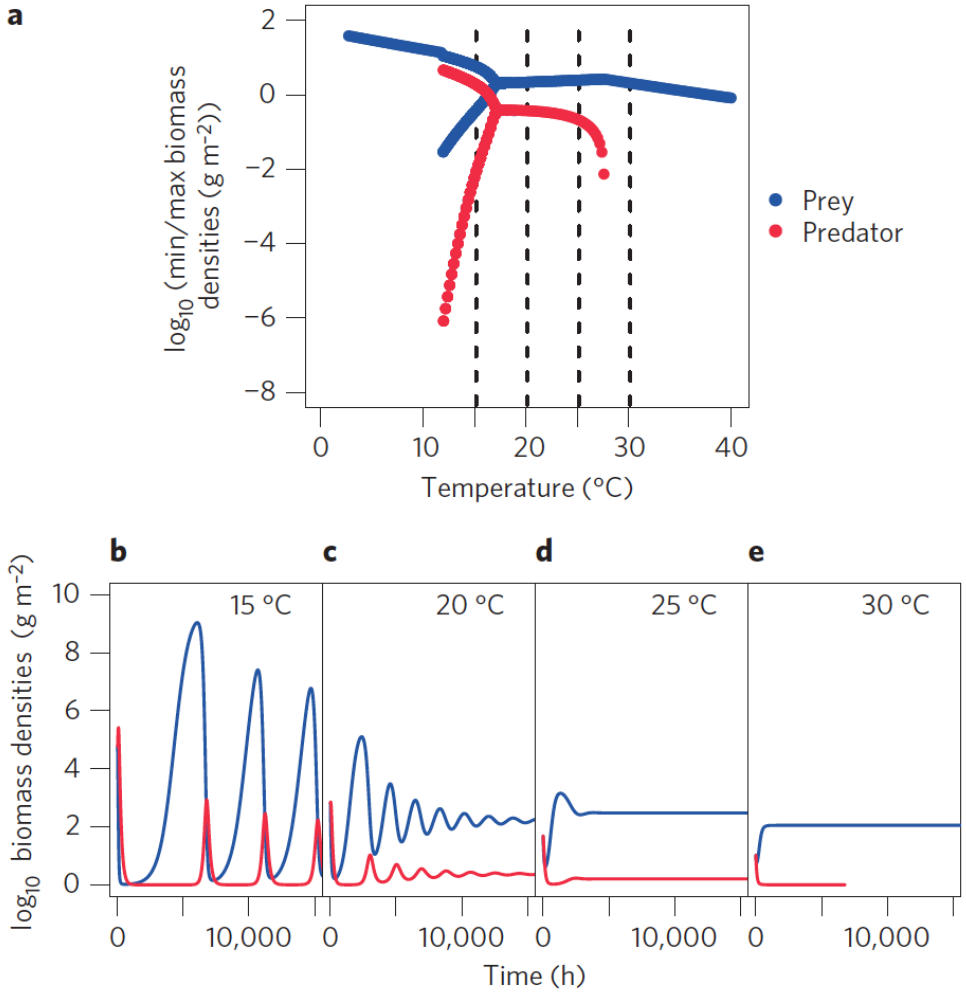

Figure 2.2 – Simulated predator-prey dynamics across temperature gradients.
a, Bifurcation diagram showing the minimum and maximum predator and prey densities within time series across a temperature gradient. Dashed lines indicate the temperatures corresponding to the exemplary time series. **b - e**, Exemplary time series at 15 ° C, 20 ° C, 25 ° C and 30 ° C. To allow comparisons with empirical data **b - e** show the first part of the time series including transient dynamics, whereas the bifurcation diagram (**a**) shows minima and maxima within the last tenth of the simulation representing long-term dynamics. The corresponding longer time series are shown in the Supplementary Information. Blue, prey densities; red, predator densities

To generalise our findings we replicated the simulations with one million random combinations of activation energies (normal distributions with mean values and standard deviations of our meta-analyses, see Figures 2.1a, b, c; resource intrinsic growth rate: 0.84 eV ± 0.4; in Appendix Table 1). A posteriori, we categorised the different outcomes according to the following aspects: whether predator-prey dynamics were stabilised or destabilised in terms of their coefficient of variation in biomass; and whether predators persisted or became extinct with increasing temperature (Figure 2.3a). The full factorial combination of these aspects resulted in four categories that were distinguished by the distribution of the four activation energies (Figure 2.3b). In contrast to previous predictions that an increase in temperature should destabilise predator-prey oscillations (Vasseur and McCann, 2005), most parameter combinations (91.1 %, Figure 2.3a) led to positive relationships between population stability and warming. Within this group, predators survived at high temperatures, in only 17.5 % of all simulations, whereas the combination of stabilising warming effects and predator extinction at high temperatures occurred in 73.8 % - thus highlighting the broad generality of our warming predictions. Notably, only a marginal minority of all simulations (8.9 %) supported the present paradigm that warming destabilises population dynamics (Figure 2.3, see Appendix Figures 1 - 4 for time series and bifurcation diagrams). The varying dynamic consequences of warming (Figure 2.3a) can be explained by different combinations of activation energies (Figure 2.3b). If activation energies of half-saturation densities are lower than those of carrying capacities, warming will destabilise predator-prey dynamics (Figure 2.3: both left columns), as predators become more efficient and exert a stronger top-down pressure. In the opposite case, if activation energies of carrying capacities are lower than those of half-saturation densities, top-down pressure is weakened and energy fluxes are reduced and thus warming will stabilise population oscillations (Figure 2.3: both right columns). In the latter case of stabilised systems, predator extinctions occur if activation energies of metabolic rates are higher than those of maximum feeding (Figure 2.3, right column), thus supporting our hypothesis of predator starvation due to energetic mismatch. Despite the strong response of empirical carrying capacities to warming (Figure 2.1c), our model analyses suggest that they have only marginal effects on population stability and predator persistence, because their distribution was similar across the four stability categories (Figure 2.3b). Overall, our interpretation is consistent with the principle of energy flux, stating that processes (here, warming) decreasing the energy flux to consumers (here, feeding) relative to their loss rate (here, metabolic rates) will stabilise population dynamics (Rip and McCann, 2011). Our results also show that continuing these processes may lead to consumer starvation. Moreover, stability implications of warming may interact with the size structure of the community (Binzer *et al.*, 2012; Brose *et al.*, 2012) that modifies energy flux patterns (Otto *et al.*, 2007). In this context, our results bridge the gap between physiological

warming studies and analyses of population stability to provide a mechanistic explanation for possible consequences of warming while stressing population stability and predator extinction as the most likely outcome.

Our approach is based on some limiting assumptions. First, we included only invertebrates (mainly arthropods) in our empirical databases (Figure 2.1c) and model analyses (Figures 2.2, 2.3), because they represent most extant species. Although studies of vertebrate activation energies revealed similar patterns in activation energies (Gillooly *et al.*, 2001; Brown *et al.*, 2004) conclusions for endotherms may differ from our results. Second, we employed random combinations of activation energies in our model analyses (Figure 2.3a), because only very few studies measured the activation energies of feeding and metabolic rate for the same species (Vucic-Pestic *et al.*, 2011; Rall *et al.*, 2012). These studies also documented very small activation energies of half-saturation densities and that metabolic rate increases more strongly with temperature than feeding. Accordingly, they represent the fourth category with population stabilisation and predator extinction (Fig. 2.3, right-most column), which supports the conclusions of our model analyses. However, our results also indicate the need to further study differences in temperature scaling for biological rates measured for the same species. Third, the empirical data in our databases are founded on short-term experiments excluding evolutionary responses to temperature changes that are beyond the scope here. Here, we offer a framework that future studies can use for disentangling evolutionary from ecological consequences of warming. Fourth, we followed previous studies (Gillooly *et al.*, 2001; Dell *et al.*, 2011) in assuming Arrhenius scaling of the biological processes with temperature, whereas they may systematically break down at critically high temperature thresholds leading to hump-shaped temperature scalings (Portner and Knust, 2007; Englund *et al.*, 2011; Rall *et al.*, 2012). Although these hump-shaped relationships should cause extinctions when critically high temperature thresholds are crossed (Portner and Knust, 2007), our results suggest that extinctions may occur even within the physiologically benign temperature range as a consequence of predator starvation despite abundant resources. Despite these limiting assumptions, our database and model analyses are offering new testable predictions for how predator-prey systems should respond to warming.

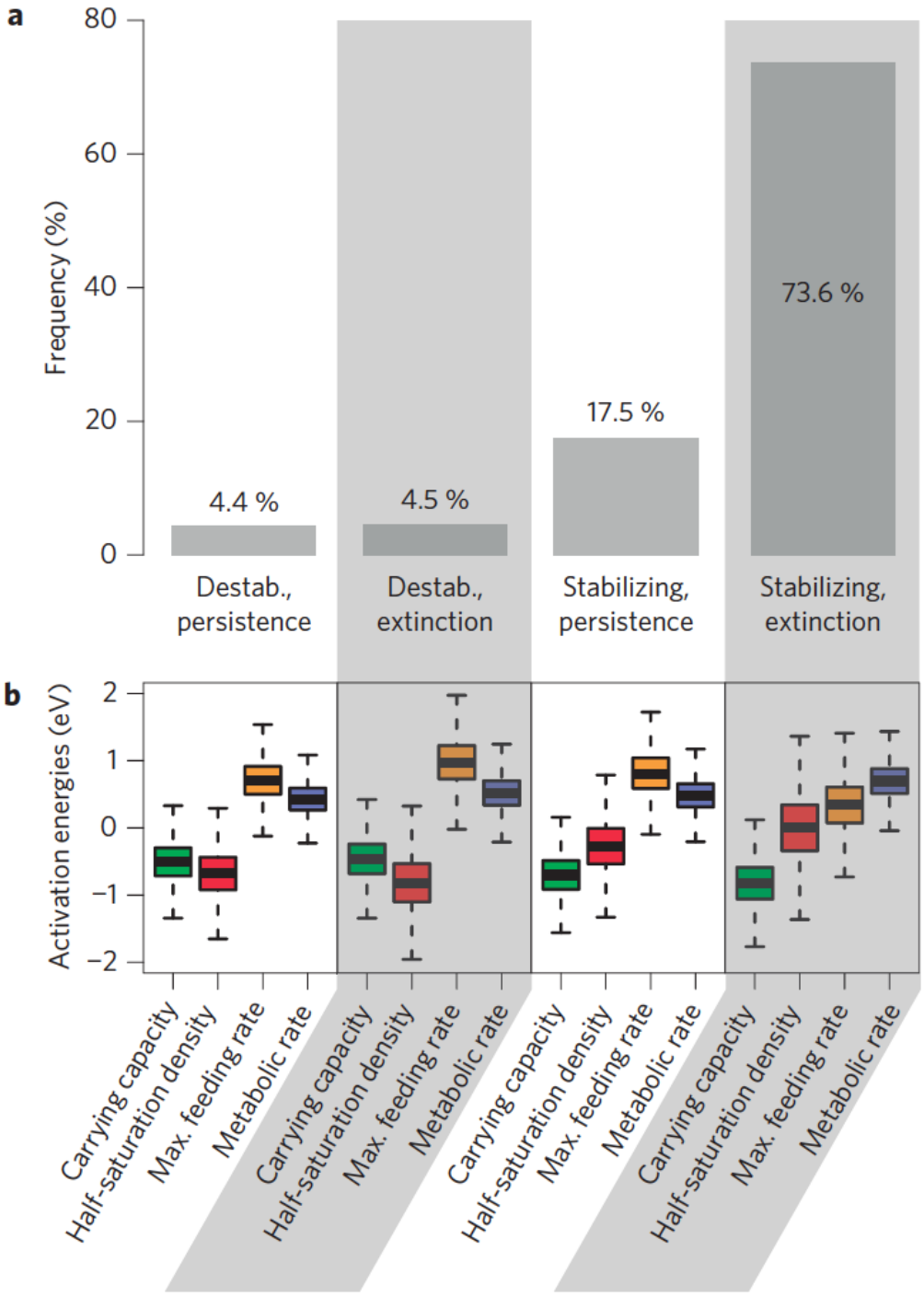

Figure 2.3 – Population stability and extinctions in simulated predator-prey systems. **a**, Percentages of possible dynamical outcomes of the simulations. Destabilising refers to an increase of the coefficient of variation of biomass, stabilising to a decrease. Persistence and extinction were measured at 40° C for the predator species. **b**, Box plot of activation energies corresponding to the categories of the dynamical outcomes shown in **a**. Outliers were excluded for graphical reasons.

We tested these predictions by measuring time series along a temperature gradient from 15° C to 30° C in a microbial predator-prey system with *Tetrahymena pyriformis* preying on *Pseudomonas fluorescens* (see Methods for detailed laboratory and statistical methods, Zuber *et al.* 2003; Jousset *et al.* 2006). Our model analyses were based on biomass dynamics, whereas we counted abundances in the microbial experiment. As cell sizes were not affected by our temperature treatments (ANOVA, p = 0.7198) the data can be compared. Our results suggest a dampening of population oscillations with warming: although predator and prey populations showed strong oscillations at 15° C (Figure 2.4a), they were dampened at higher temperatures (20° C, Figure 2.4b). At 25° C (Figure 2.4c), two alternative states occurred: in two of three replicates ciliate predators persisted with both species showing lower oscillation amplitudes (Figure 2.4c, Appendix Figure 5c and g), whereas in the third replicate the predator population became extinct (Appendix Figure 5k). At this temperature, the fragile predator-prey system was on the verge between persistence and extinction. At 30° C (Figure 2.4d), predators in all treatments became extinct. Statistically, minima and maxima of bacteria both decreased from 15° C to 25° C with maxima showing a steeper decrease than minima ($E_{min,t=0}$ = -0.53, p < 0.001; $E_{max,t=0}$ = -0.64, p < 0.001). Ciliate minima increased and their maxima decreased ($E_{min,t=0}$ = 0.27, p < 0.001; $E_{max,t=0}$= 0.50, p < 0.001). These statistically significant patterns in the activation energies of minima and maxima demonstrated that the amplitudes of the predator and the prey oscillations decreased with warming (Figure 2.4e).

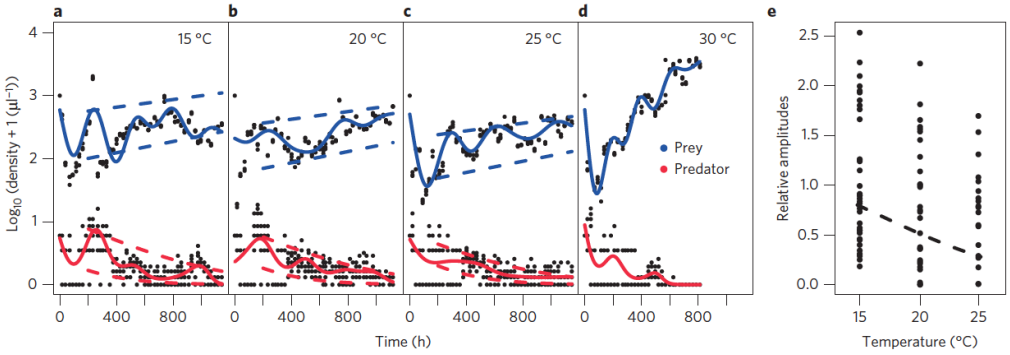

Figure 2.4 – Laboratory time series of the predator *T. pyriformis* (red lines) and its prey *P. fluorescens* CHA19-gfp (blue lines).

a-d, Replicates of the time series at 15° C, 20° C, 25° C and 30° C were fitted with a GAM with a Poisson distribution. Dashed lines in the related colours show quantile regressions indicating the minima and maxima of abundances. **e**, Relative amplitudes of both predator and prey time series dependent on temperature. The dashed line denotes the regression line according to an average amplitude sequence number (which is 4); see Appendix for details.

The experimental data thus confirmed the model predictions that warming stabilises predator-prey dynamics by dampened oscillations, whereas predators become extinct at high temperatures. Our analyses of global databases, model simulations and empirical microcosm experiments show that warming generally stabilises population dynamics in predator-prey systems on ecological timescales. This is due to a mismatch between metabolic rate and realised feeding caused by: constant foraging efficiencies (that is, half-saturation densities) while prey densities (that is, carrying capacities) decrease; and increases in metabolic rate exceeding those of maximum feeding rates. Beyond a threshold temperature, the decreasing energetic efficiency with warming will cause extinction of predators owing to starvation. This contrasts with the present paradigm that warming causes extinctions by increased oscillations (Vasseur and McCann, 2005). Our results provide evidence that populations on the verge of extinction are characterised by minimal oscillations or even equilibrium dynamics. Thus, our results increase the predictability of warming effects and illustrate the risk of predator extinction waves in a warmed world.

Methods

Database

We used published databases on metabolic rates (Ehnes *et al.*, 2011; White *et al.*, 2006) and functional response parameters (Rall *et al.*, 2012) and extended them by protozoan metabolic rates and maximum population densities (Appendix). Only data sets containing three or more temperature levels differing by two or more degrees Kelvin were included. To analyse data only within the biologically relevant temperature range (Savage *et al.*, 2004) we deleted the lowest and/or highest measurements in cases where hump-shaped deviations occurred. We carried out an ordinary least-squares regression on each data set to obtain activation energies (see Appendix for details).

Simulations

Consistent with previous model studies (Yodzis and Innes, 1992; Vasseur and McCann, 2005; Otto *et al.*, 2007; Brose *et al.*, 2006; Binzer *et al.*, 2012), we used a bioenergetic population model for the simulations where the biomass changes (B'_{prey} and $B'_{predator}$) follow

$$B'_{prey} = GB_{prey} - B_{predator}F \tag{2.2}$$

$$B'_{predator} = \epsilon B_{predator}F - xB_{predator} \tag{2.3}$$

where B_{prey} and $B_{predator}$ are the biomass densities of the prey and the predator species, respectively. G is the resource's logistic growth term, F is the feeding term, ϵ is the assimilation efficiency and x is the predator's metabolic rate (see Appendix for details). As in previous biomass models, biomass loss due to metabolic rate (biomass loss of individuals) or mortality (loss of individuals) is not differentiated.

Organisms and culture conditions

We used as bacterial prey *P. fluorescens* CHA19, a gacS-isogenic mutant of *P. fluorescens* CHA0, chromosomally tagged with green fluorescent protein (Jousset *et al.*, 2006) (GFP). This strain does not produce secondary metabolites, which allows monitoring of trophic interactions without toxin-related interferences. Bacterial stocks were kept frozen at -8° C. Before the experiment, bacteria were grown on lysogeny broth plates supplemented with 25 $\mu g\ ml^{-1}$ kanamycin. One single colony was picked and cultured overnight at 20° C in liquid lysogeny broth, collected by centrifugation (13,000 r.p.m., 10,000 g for one minute) and washed three times in 1:10 modified Ornston and Stanier minimal medium supplemented with 1 mM glycerol as sole carbon source.
As predators we used the bacterivorous protozoa *T. pyriformis* CCAP 1630/1W. Protozoa were kept in axenic cultures in proteose peptone yeast extract medium containing 20 g proteose peptone and 2.5 g yeast extract per litre at 14° C for at least five days until reaching sufficient concentrations. Before the experiments, protozoa were collected by gentle centrifugation three times (300 r.p.m., 400 g, 0° C, for seven minutes) and resuspended in 1:10 Ornston and Stanier 1 mM glycerol medium.

Time-series experiments

Time-series experiments were conducted in 100 ml Ornston and Stanier 1:10 0.1 mM glycerol in 250 ml Erlenmeyer borosilicat glass flasks closed with aluminium caps. Flasks were incubated in thermostatic cabinets (Lovibond, Tintometer GmbH) with agitation (200 r.p.m.) at 15° C, 20° C, 25° C and 30° C. Start concentrations of *P. fluorescens* CHA19-GFP were 1,000 cells per microlitre, whereas *T. pyriformis* concentrations were 5 cells per microlitre in each treatment. Every day, 10 ml of the culture were removed for analysis and replaced with fresh medium. Bacterial counts were determined in a C6 flow cytometer (Accuri) from three 150 μl aliquots. Bacteria were gated on the basis of their SSC-A x FL1-A signal; 50,000 events per sample were recorded. If counts exceeded 5,000 events per second, samples were diluted accordingly. *T. pyriformis* were counted in an improved Neubauer (> 10 cells per microlitre) or a Fuchs-Rosenthal (<10 cells per microlitre) counting chamber.

Time-series analysis

We analysed each time series through generalised additive models (Wood 2011; GAMs) and generalised linear models to analyse both the amplitude and general average trend of the times series. As populations are integers and our data showed overdispersion, we used quasipoisson models. Subsequently, we simulated 1,000 data points for each time series according to the single model results through the predict function in *R*. We divided the results of the GAM model by the results of the generalised linear model to calculate the normalised time-series values. We subsequently analysed at what time-step extrema of the population densities occurred (Kim and Oh, 2013) and calculated the resulting normalised amplitudes. We added the corresponding sequence number of the amplitude within an independent time series for further analyses (that is, amplitude 1, amplitude 2). Amplitude strength was analysed using ln-transformed normalised amplitudes as a function of sequence number, Arrhenius temperature and squared Arrhenius temperature and the interaction between both temperature terms with the amplitude sequence number. To ensure independence of data, we used linear mixed-effects models (**?**) with time-series identity and nested taxonomic group as random effects as well as a temporal correlation of the dependence of amplitudes to amplitude sequence number (corAR1(); Zuur 2009). We selected models according to the penalised log-likelihood (Akaike's Information Criterion) using maximum likelihood (method = ML) while subsequently testing the resulting model again with the restricted estimates maximum likelihood method (method = REML; Zuur 2009). Furthermore, we analysed how minima and maxima of these predicted average time series behave with temperature and time for systems where the predator survived and systems where the predator went extinct by using the quantile regression at a level of 0.05 and 0.95 (function *qr* in *R*). To avoid transient dynamic effects, we deleted the first 200 h from the predicted values.

Acknowledgement

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Chapter 3.

Interactive effects of shifting body size and feeding adaptation drive interaction strengths of protist predators under warming

Katarina E. Fussmann, Benjamin Rosenbaum, Ulrich Brose, Björn C. Rall

Abstract

Global change is heating up ecosystems fuelling biodiversity loss and species extinctions. High-trophic-level predators are especially prone to extinction due to an energetic mismatch between increasing feeding rates and metabolism with warming. Different adaptation mechanisms such as decreasing body size to reduce energy requirements (morphological response) as well as direct effects of adaptation to feeding parameters (physiological response) have been proposed to overcome this problem. Here, we use protist-bacteria microcosm experiments to show how those adaptations may have the potential to buffer the impact of warming on predator-prey interactions. After adapting the ciliate predator *Tetrahymena pyriformis* to three different temperatures (15° C, 20° C and 25° C adaptation temperature) for approximately 20 generations we conducted functional response experiments on bacterial prey along an experimental temperature gradient (15° C, 20° C and 25° C experimental temperature). We found an increase of maximum feeding rates and half-saturation densities with rising experimental temperatures. Adaptation temperature had on average slightly negative effects on maximum feeding rates, but maximum feeding rates increased more strongly with rising experimental temperature in warm adapted predators than in cold adapted predators. There was no effect of adaptation temperature on half-saturation densities characterising foraging efficiency. Besides the mixed response in functional response parameters, predators also adapted by decreasing body size. As smaller predators need less energy to fulfil their energetic demands, maximum feeding rates relative to the energetic demands increased slightly with increased adaptation temperature. Accordingly, predators adapted to 25° C showed the highest feeding rates at 25° C experimental temperature, while predators adapted to 15° C showed the highest maximum feeding rate at 15° C. Therefore, adaptation to different temperatures potentially avoids an energetic mismatch with warming. Especially a shift in body size with warming additionally to an adaptation of physiological parameters potentially helps to maintain a positive energy balance and prevent predator extinction with rising temperatures.

Introduction

Global change has a negative impact on biodiversity, up to a point where scientists consider the world to be on the verge of the sixth wave of mass extinction (Wake and Vredenburg, 2008; Pereira *et al.*, 2010; Barnosky *et al.*, 2011). Changing temperatures are one major driver of climate change and are expected to have a global impact (MEA, 2005). Climate reports predict a minimum increase of 1.5° C in surface temperature by the end of the century and it is deemed extremely likely that anthropogenic causes (Cook *et al.*, 2013) have led to the warmest 30 year period of the last 1,400 years (IPCC, 2014). Temperature directly affects development, survival, range and abundance of species (Bale *et al.*, 2002) and has a strong effect on species interactions (Montoya and Raffaelli, 2010) and on the structure and dynamics of species communities (Brose *et al.*, 2012). Further, increasing temperatures in aquatic as well as terrestrial ecosystems have been linked to vast biodiversity losses during extinction waves in earlier earth periods (Gómez *et al.*, 2008; Mayhew *et al.*, 2008; Joachimski *et al.*, 2012). Despite this negative impact of high temperatures on taxonomic richness, previous periods of warming have also been associated with high speciation rates since increasing temperatures can trigger rapid evolution (Gillooly *et al.*, 2005; Geerts *et al.*, 2015) and create niche openings by eliminating species previously occupying a certain habitat or resource (Mayhew *et al.*, 2008). This leads to the question whether adaptation and evolution pose a feasible escape from warming induced extinction. Species' extinctions and therewith biodiversity strongly depend on the stability of the ecosystems they are embedded in (May, 1972; McCann, 2000). Stability furthermore depends on the interaction strengths between species. High interaction strengths decreases the population stability leading to extinction caused by high population cycles, and too low an interaction strength may lead to extinction of predators due to starvation (Rall *et al.*, 2010).

The functional response is one of the oldest and most established tools to quantify the strength of these interactions and describe species-species feeding interactions in ecology (Holling, 1959*b*; Jeschke *et al.*, 2002). In this framework, the feeding rate, F, of a predator depends on the density of its resource. The functional response, as described by Real (1977) includes a non-linear feeding rate, which determines the maximum feeding, f, when prey is abundant. At lower prey densities the functional response curve is characterised by the predator's foraging efficiency. Mathematically this is described by half-saturation density, η, the prey population density at which half of the maximum feeding rate is reached (Figure 3.1). These parameters can be used to evaluate interspecies interaction strength which have been a main predictor of ecosystem stability (Berlow *et al.*, 2009).

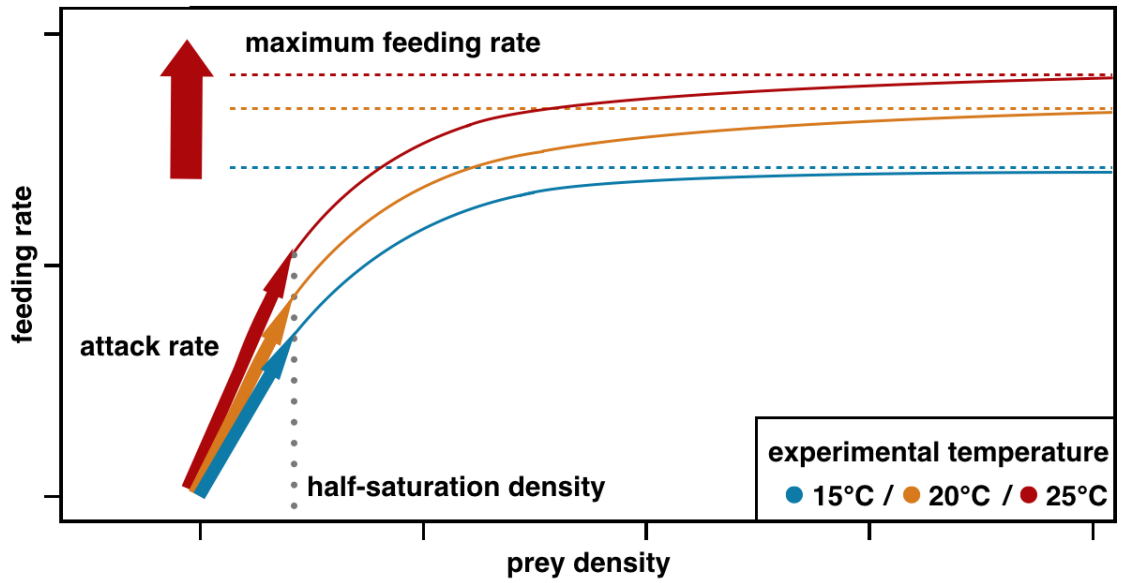

Figure 3.1 – Expected trends for changes in maximum feeding rate (dashed lines) and half-saturation density (dotted line) with increasing temperatures based on previous studies (Rall *et al.* 2012; Fussmann *et al.* 2014; Chapter 2). Maximum feeding rates are likely to increase with experimental temperature, while half-saturation densities have a variable scaling relationship being on average neutral. Maximum feeding rates of predators adapted to higher temperatures are expected to increase to cope with increasing metabolic demands with the highest maximum feeding rates at high temperatures and vice versa for cold adapted predators. Half-saturation densities are expected to not be influenced by temperature adaptation resulting in an increase of attack rates (arrows) at low prey densities in warm adapted predators to facilitate higher maximum feeding rates at high prey densities.

To investigate the effects of warming on interaction strength, previous studies have used the principles of the Metabolic Theory of Ecology (MTE; Gillooly *et al.* 2001; Brown *et al.* 2004) which is quantified as activation energies measured in electron Volt $[eV]$ according to the Arrhenius equation (Arrhenius, 1889). The Arrhenius equation, originally used to describe chemical reactions and enzyme kinetics, has become a mechanistic model for biological rates in ectotherm organisms (Gillooly *et al.*, 2001; Brown *et al.*, 2004; Savage *et al.*, 2004). The MTE argues that all biological rates as well as higher order patterns such as density distributions scale with temperature. Therefore, the parameters of the functional response, determining interaction strength should follow the same principles (Vasseur and McCann 2005; Fussmann *et al.* 2014; Chapter 2): maximum feeding rates are often assumed to scale with temperature in the same manner as metabolic demands with an activation energy ranging from 0.6 to 0.7 eV across different taxa (Vasseur and McCann, 2005). This is corroborated by empirical data of ciliates, flagellates and other microfauna showing even higher activation energies for maximum feeding rates of $0.772eV$ (Hansen *et al.*, 1997; Vasseur and McCann, 2005). However, a broader analysis of predators from different ecosystems revealed that maximum feeding, f, scales with an activation energy of

roughly 0.3 to $0.4eV$ (Rall *et al.* 2012; Fussmann *et al.* 2014; Chapter 2). This leads to a mismatch where, under warming, metabolism increases faster than maximum feeding. As a result, predators cannot meet their metabolic demands and run the risk of starvation even if they are surrounded by prey (Vucic-Pestic *et al.* 2011; Fussmann *et al.* 2014; Chapter 2). The half-saturation density, η, can be influenced by a variety of parameters such as encounter rate, mobility of prey and predator, and search efficiency. Most significantly, mobility of prey and predator and therefore encounter rates and search efficiencies are influenced by warming (Sentis *et al.*, 2012; Dell *et al.*, 2014). Since the reaction of prey as well as predator to changing temperatures can be highly variable in both, general tendency and intensity, this results in a high variability of activation energies for half-saturation density, ranging from positive to negative relationships with warming, being on average neutral (Fussmann *et al.* 2014; Chapter 2). Constant half-saturation densities can be mechanistically explained by a simultaneous increase of feeding at low densities (the "rate of successful attacks" (Holling, 1959*b*), often referred to as attack rate, capture rate or maximum clearance rate) and maximum feeding rate with increasing temperatures. At high temperatures, natural systems show lower prey population densities due to reduced resource availability (Brown *et al.* 2004; Meehan 2006; Fussmann *et al.* 2014; Chapter 2). If predator abundances are low in natural systems and predators are not able to increase their foraging efficiency under those conditions (i.e. decrease of half-saturation densities) feeding rates eventually decrease. These mismatches can lead to the loss of higher trophic levels due to starvation (Binzer *et al.* 2012; Fussmann *et al.* 2014; Chapter 2) and decreases in biodiversity due to warming (Binzer *et al.*, 2016).

Other mechanisms, for example adaptation to higher temperatures, may be able to counteract starvation due to energetic mismatch (Angilletta Jr., 2009; Chevin *et al.*, 2010; Somero, 2010). In studies where adaptation may have buffered the physiological impacts of warming, temperature had hardly any effect on the overall fitness of a population (Chown *et al.*, 2010). Adaptation in predator-prey systems is often studied from a prey's perspective (McPeek *et al.*, 1996; Yoshida *et al.*, 2003; Abrams and Walters, 2010) but rarely from a predator's (Sentis *et al.*, 2015), despite them being most affected by temperature changes (Rall *et al.*, 2010; Binzer *et al.*, 2012; Fussmann *et al.*, 2014). Given that predator energy efficiency is a major determinant of population stability (Vasseur and McCann, 2005; Rall *et al.*, 2010), an adaptation of either metabolism or functional response parameters or both could be crucial. Temperature adaptation, however, is often investigated on short time scales (Sentis *et al.*, 2015) leading to concerns that the time frame of temperature changes exceeds adaptation rates (Quintero and Wiens, 2013). Generally, short-term studies tend to underestimate a species' capability of adapting to climate change (Leuzinger and Thomas, 2011). In a short-term study focussing on acclimation within one generation, the physiological temperature effect on feeding rates proved crucial since metabolic rates and

body size were less affected by acclimation temperature (Sentis *et al.*, 2015). However, metabolism and functional response parameters are not only influenced by temperature but also by body size (Vucic-Pestic *et al.*, 2011; Ott *et al.*, 2012; Rall *et al.*, 2012; Kalinkat *et al.*, 2013), and, body size itself is influenced by temperature (Atkinson 1994, Figure 3.2). Globally, species in warmer regions tend to have smaller average body sizes than species in colder ecosystems (Bergmann, 1847), this trend was also documented in warming studies investigating different size spectra of local freshwater communities (Daufresne *et al.*, 2009; Yvon-Durocher *et al.*, 2011). Further, body size has been shown to have a strong effect on interaction strengths through allometric scaling (Brose, 2010). Smaller body sizes require less energy to maintain metabolism and population growth (Brown *et al.*, 2004) leading to reduced maximum feeding rates while not affecting the half-saturation densities (Hansen *et al.*, 1997). The half-saturation density ($\eta = 1/(T_h a)$) can be calculated as the inverse of the product of handling time ($T_h = 1/f$) and attack rate ($a = f/\eta$). Consequently, if maximum feeding rates and attack rates scale similarly with body size, the effect on half-saturation density is equalled out ($\eta = f/a$) (Rall et al., 2012). As a result of constant half-saturation density, maximum feeding rates are constant across the entire prey density gradient (Figure 3.1).

Here, we explored how interactive effects of direct temperature adaptation of feeding rates and indirect effects on feeding rates through temperature induced changes in body size influence functional response parameters. We designed a microcosm experiment with short generation times (Callahan *et al.*, 2008) to understand how adaptation to different temperatures over 20 generations influences feeding behaviour. We investigated whether adaptation to temperature enables predator populations to avoid extinction caused by crossing the threshold where metabolic demands overtake the energy intake through feeding. (1) We expect body sizes of warm adapted *Tetrahymena* to decrease within 20 generations compared to predators adapted to colder temperatures (Figure 3.2 a). (2) Half-saturation densities should not be affected by increasing experimental temperature. If *Tetrahymena* adapts both, attack rates and maximum feeding rates simultaneously, we expect no change in half-saturation density with adaptation temperature (Figure 3.2 b). (3) The change in body size, (cell size) will cause a decrease in maximum feeding rates and attack rates in warm adapted predators. Body size, however, will not affect the temperature dependency of these rates or change the activation energies (Figure 3.2 c - body size mediated feeding adaptation). (4) We assume that the direct physiological adaptation of maximum feeding rates and attack rates leads to a change of activation energies: warm adapted predators should show the steepest increase (highest activation energy) as they should be well adapted to higher temperatures. Predators adapted to lower temperatures should have the highest feeding rates at cold temperatures but will not or just marginally be able to increase feeding with increasing temperature (Figure 3.2 d - direct feeding adaptation). These

different scalings will result in a statistically significant interaction. (5) If both mechanisms occur simultaneously, maximum feeding rates and attack rates should be lowest for warm adapted predators and increase with decreasing adaptation temperature while keeping the interactive direct effect of adaptation (Figure 3.2 e - realised feeding adaptation).

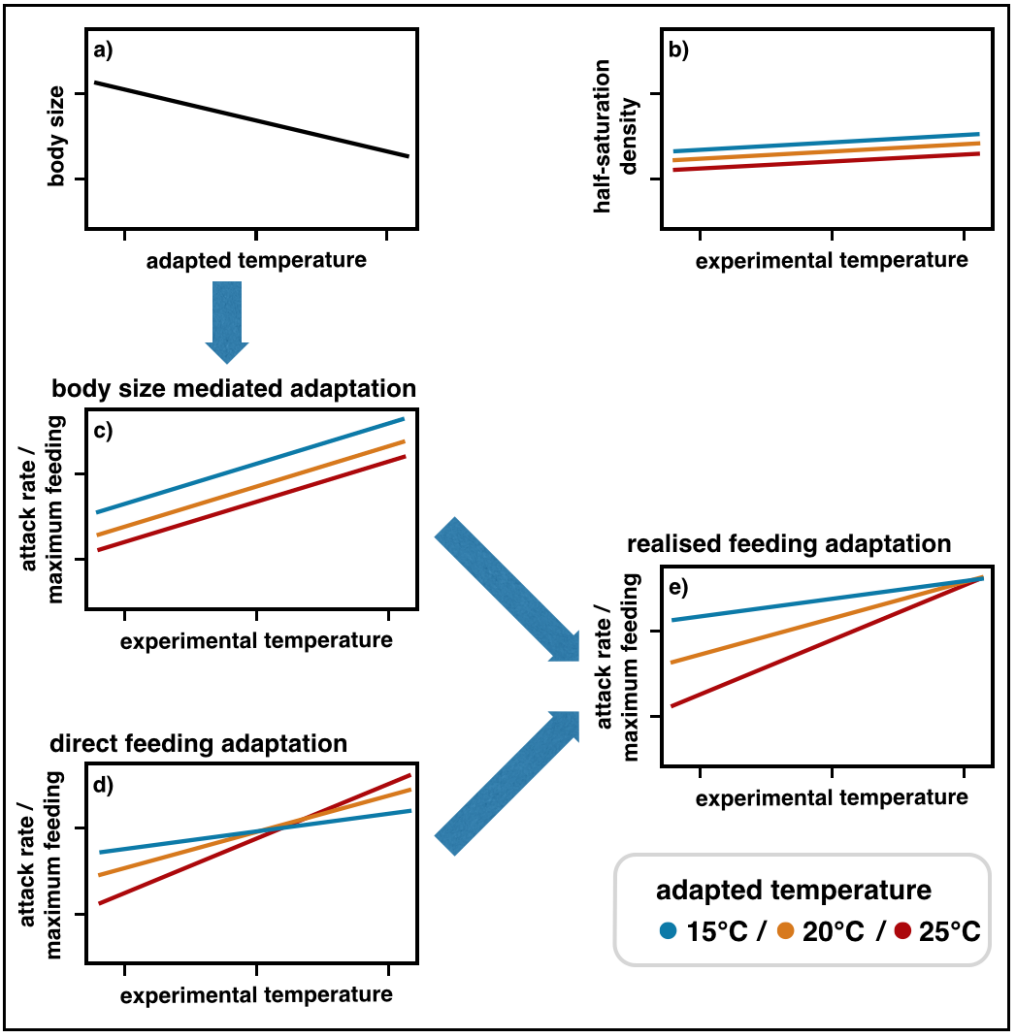

Figure 3.2 – **a) Predator body size** (cell size) decreases with increasing adaptation temperature. b) Half-saturation densities are not expected to change with experimental or adaptation temperature. **c) Body size mediated adaptation**: Decreasing predator body size with increasing adaptation temperatures generally reduces maximum feeding rates in warm adapted predators with an assumed scaling exponent of 0.75 (Brown *et al.*, 2004). **d) Direct feeding adaptation**: Maximum feeding rates generally increase with rising experimental temperatures. Adaptation to temperature leads to a direct feeding adaptation of maximum feeding rates. Predators adapted to 15°C are expected to show the overall highest maximum feeding at 15°C experimental temperature, while predators adapted to 25°C should have the overall highest maximum feeding rates at 25°C. **e) Realised feeding adaptation**: Realised feeding adaptation shows the interactive effects of body size mediated adaptation and direct feeding adaptation on maximum feeding rates.

Methods

Laboratory cultures

We chose a model predator-prey system with the non-toxic bacterium *Pseudomonas fluorescens* CHA19 (Zuber *et al.*, 2003; Weller *et al.*, 2007) as prey and the ubiquitous, predatory ciliated protozoan *Tetrahymena pyriformes* CCAP 1630/1W (CCAP Culture Collection of Algae and Protozoa, SAMS Limited, Scottish Marine Institute, Scotland, United Kingdom).
Pseudomonas fluorescens CHA19 was marked with GFP using a Mini-TN7 transposon I (Lambertsen *et al.*, 2004). After molecular cloning, one colony of the *Pseudomonas* strain was deep frozen at -80° C in a 25 % glycerol solution. For every experiment a small sample was defrosted and incubated on LB-Agar containing 8 $\mu g/l$ gentamycin before single colonies were incubated at room temperature in selective LB-medium over night. *Tetrahymena* was grown in 2 % proteone peptose medium at 20° C. At the start point of the adaptation experiment, the culture of *Tetrahymena* was divided equally into 9 cultures, 3 cultures were henceforth kept at 15° C, three cultures were kept at 20° C and three cultures were kept 25° C. A temperature range between 15° C and 25° C is realistic for temperate aquatic systems in absence and presence of an extreme temperature event (Seifert et al., 2015). For all adaptation temperatures, exponential growth rates of *Tetrahymena pyriformis* were measured to estimate the timeframes until approximately 20 generations were reached and functional response experiments were conducted (Figure 7). For predators kept at 15° C adaptation temperature, this was approximately 18 days, while for warmer adapted predators this time span was approximately 13 and 12 days for 20° C and 25° C adaptation temperature, respectively. 20 generations is consistent with other studies ranging from only one generation (Sentis *et al.*, 2015) to 10 and 100 generations (Padfield *et al.*, 2015). To reduce the traces of medium prior to the functional response measurements bacteria were centrifuged (13.000 rpm x 1 min) and re-suspended three times in sugarless Ornston and Stannier (OS) medium (Ornston, 1966) diluted with ddH_2O 1 : 10. Bacterial counts were measured using an Accuri C6 flow cytometer (BD Biosciences) on slow with an FSC-H of 8000 and a SSC-H of 2000. Ciliates were harvested by centrifugation at 300 rpm for 7 min at 0° C and re-suspended in OS medium three times. Prior to functional response experiments the predators were starved for 12 hours at their respective adaptation temperatures. The number of ciliates and their body sizes were measured with a Beckman Coulter Counter Multisizer 4 with a 100 μl aperture on slow fluidics speed (Beckman Coulter, Inc.).

Functional response experiments

Functional response experiments were conducted in 96-well plates. One column contained only the ciliated predator *Tetrahymena*, each of the remaining 11 columns contained a different bacterial prey density, with six rows as identical replicates and two rows as bacterial controls. Each well contained 200 μl of sugar-free OS 1:10 media, prey densities ranged from 34778 bacteria μl^{-1} to 1189416 bacteria μl^{-1}, while predator abundances were kept constant at 100 predators μl^{-1}. We used a fully factorial design for the functional response experiments, conducting experiments at the full experimental temperature range of 15° C, 20° C and 25° C with all three cultures of all adaptation temperatures after approximately 20 generations (Figure 7). Fluorescence intensities of bacteria were measured at two time points, after four hours into the experiment to avoid transient dynamics and at the end of the experiment, three hours thereafter, in an Infinite M200 plate reader (Tecan, Männedorf, Switzerland). After orbital shaking for 10 seconds, each well was measured with an excitation wavelength of 485 nm and an emission wavelength of 520 nm reading 15 flashes with a manual gain of 100. To standardise a reliable value for bacterial abundance from the GFP signal measured in the plate reader, comparative measurements were taken using a plate reader and flow cytometer with an FSC-H of 8000 and SSC-H of 2000 and slow fluidics speed.

Calculation of bacterial densities

We assessed bacterial fluorescence data by using a regression tree (tree-function, Ripley 2016) classifying count-fluorescens relationships (Figure 8). To estimate the bacterial density we first fitted the ln-transformed fluorescence signal measured in the plate reader against the ln-transformed number of cells measured with the flow cytometer (independent variable). All fluorescence values below a ln(GFP) of 6.03068 and a ln(count) of 9.071045 and above a ln(GFP) of 9.37609 and a ln(count) of 13.15602 were excluded from further analysis since we could not guarantee the proportionality between cell count and fluorescent signal beyond these counts. We then calculated bacterial abundance by predicting a linear model with GFP signal and experimental temperature as independent variables. To account for background signals, all experimental data was blanked against OS 1:10 ddH_2O experimental media and treatments containing only the predator *Tetrahymena pyriformis*. This resulted in 141 control treatments containing only bacterial prey, and 306 functional response experiments that were used for further analysis (Table 5).

Functional response

The functional response describing the non-linear feeding rate, F, is defined as Real (1977):

$$F = \frac{fN}{\eta + N} \ , \tag{3.1}$$

where N is the prey density, f is the maximum feeding rate and η is the half-saturation density. In our experiment, additional to a constant decline of prey through time due to feeding, natural growth and mortality of the bacterial prey occurred in control experiments. We therefore decided to incorporate the Gompertz growth for microbiological systems (Gompertz, 1825; Paine *et al.*, 2012)

$$G = rNln\frac{K}{N} \ , \tag{3.2}$$

where r is the intrinsic growth rate of bacteria and K is the carrying capacity of bacteria. A model accounting for changes in prey abundance over time due to feeding as well as natural prey growth or death is expressed in the following ordinary differential equation (ODE):

$$\frac{dN}{dt} = \frac{-fN}{\eta + N}P + rNln\frac{K}{N} \ , \tag{3.3}$$

where the change in prey abundance over time t is characterised by the functional response model; P is the predator density. To account for changes of the parameters with experimental temperature we calculated Arrhenius temperatures and activation energies $E_{f,\eta}$:

$$f = f_0 e^{E_f \frac{(T_e - T_0)}{kT_e - T_0}} \ , \tag{3.4}$$

$$\eta = \eta_0 e^{E_\eta \frac{(T_e - T_0)}{kT_e - T_0}} \ , \tag{3.5}$$

where f_0 and η_0 are normalisation constants, T_e $[K]$ is the absolute experimental temperature, T_0 $[K]$ is the normalisation temperature and k $[eVK^{-1}]$ is the Boltzmann's constant yielding the well known Arrhenius equation (Arrhenius, 1889; Gillooly *et al.*, 2001). Additionally, growth and carrying capacity also scale with temperature (Gillooly *et al.*, 2001; Savage *et al.*, 2004):

$$r = r_0 e^{E_r \frac{(T_e - T_0)}{kT_e - T_0}} \ , \tag{3.6}$$

$$K = K_0 e^{E_K \frac{(T_e - T_0)}{kT_e - T_0}} \ , \tag{3.7}$$

with r_0 and K_0 being normalisation constants, and E_r and E_K being the experimental activation energies. To investigate the effects of adaptation, we extended the Arrhenius equation using a term describing the dependency of the maximum feeding rate, f, and of the half-saturation density, η, on the temperature the predator was adapted to T_a:

$$f = f_0 e^{E_f \frac{(T_e - T_0)}{kT_e - T_0}} e^{A_f \frac{(T_a - T_0)}{kT_a - T_0}} \ , \tag{3.8}$$

$$\eta = \eta_0 e^{E_\eta \frac{(T_e - T_0)}{kT_e - T_0}} e^{A_\eta \frac{(T_a - T_0)}{kT_a - T_0}} \ , \tag{3.9}$$

where A_f and A_η are the activation energies for temperature adaptation. Both, maximum feeding and half-saturation density may interactively react to both, experimental and adaptation temperature (i.e. $E_{f,\eta}$ is different for different T_a). We therefore introduced an interaction term, $I_{f,\eta}$, into equation 3.8, 3.9 (i.e. statistical interaction term), yielding:

$$f = f_0 \ e^{E_f \frac{(T_e - T_0)}{kT_e - T_0}} \ e^{A_f \frac{(T_a - T_0)}{kT_a - T_0}} \ e^{I_f \frac{(T_e - T_0)}{kT_e - T_0} \frac{(T_a - T_0)}{kT_a - T_0}} \ , \tag{3.10}$$

$$\eta = \eta_0 \ e^{E_\eta \frac{(T_e - T_0)}{kT_e - T_0}} \ e^{A_\eta \frac{(T_a - T_0)}{kT_a - T_0}} \ e^{E_\eta \frac{(T_e - T_0)}{kT_e - T_0} \frac{(T_a - T_0)}{kT_a - T_0}} \ . \tag{3.11}$$

Further, we calculated realised activation energies for maximum feeding rates $\tilde{E}_f$ of the experimental temperature for each adaptation temperature:

$$\tilde{E}_f = E_f + I_f \frac{(T_a - T_0)}{kT_a - T_0} \ . \tag{3.12}$$

Maximum feeding rates, f, scale not only with temperature but also with body size with a power-law exponent of 0.75 according to the MTE (Yodzis and Innes, 1992; Brown *et al.*, 2004). Half-saturation densities, η, can be defined as the quotient of maximum feeding rate and attack rate ($\eta = f/a$, Koen-Alonso 2007), where both parameters share the same power law exponent of 0.75 (Brown *et al.*, 2004) and do not scale with body size (Yodzis and Innes, 1992; Hansen *et al.*, 1997). The body size dependent functional response can therefore be described with a 3/4 power law scaling of the maximum feeding rate, f, with

body size, m:

$$F = \frac{(fm^{0.75}N}{\eta + N} = \frac{fN}{\eta + N} m^{0.75} \ . \tag{3.13}$$

To demonstrate the effect of direct feeding adaptation (Figure 3.2 d - direct feeding adaptation), we corrected our fitted results based equation on equation 3.8 (see below and in the Appendix a description of the fitting methods) by dividing feeding rates by the metabolic body size of the predator (Schmitz and Price, 2011; Schneider *et al.*, 2012):

$$f_m = f_0 \ e^{E_f \frac{(T_e - T_0)}{kT_e - T_0}} \ e^{A_f \frac{(T_a - T_0)}{kT_a - T_0}} \ e^{I_f \frac{(T_e - T_0)}{kT_e - T_0}} \ \frac{(T_a - T_0)}{kT_a - T_0} / m^{0.75} \ . \tag{3.14}$$

Mean ciliate body size [μm^3], adapted to the respective temperatures at the time of experiment after an adaptation period of approximately 20 generations, was measured in the Beckmann Coulter Counter. Note that this calculation was done after fitting the functional response model to the data. This method to correct for body size differences in temperature dependent functional response parameters was already successfully applied in prior studies (Sentis *et al.*, 2012, 2014).

Fitting algorithm

We used Bayesian methods for parameter estimation (equation 3.3 including scaling relationships for r, K, f and η). Data of prey densities after 4 hours $N(t_4)$ were used as initial values for the numerical solution of the ordinary differential equations (ODE) and data of densities after 7 hours $N(t_7)$ were modelled using ln-normally distributed errors. Model parameters for control treatments and treatments with predators present were estimated within the same model. Samples from the posterior distribution of the parameters given the data were drawn using Hamiltonian Monte Carlo sampling in Stan, accessed via the RStan package (Stan Development Team, 2016). The Stan software comes with a built in ODEsolver, making it suitable for fitting ODE-based functional responses (equation 3.3). We used normally distributed uninformative priors with zero means and standard deviations of 100,000 for K_0 and η_0, standard deviations of 100 for all other model parameters and a uniform distribution on the interval between 0 and 100 as a prior for the model's standard error. The parameters r_0, K_0, f_0, and η_0 were provided with a lower boundary of zero. We ran 5 Markov chains in parallel with an adaptation phase of 1,000 iterations and 20,000 sampling iterations each, summing up to 100,000 samples of the posterior distribution. Visual inspection of the trace plots and density plots showed a good mixture of the chains. Values of $\hat{R}$ sufficiently close to 1 and an adequate effective sample mass n_{eff} further verified convergence (Appendix, Table 7). We tested different models for

including adaptation temperature in the scaling relationships of f and η (Table 3.1). For model comparison we used the Watanabe-Akaike information criterion (WAIC), which can be computed from the log-likelihood values of the posterior samples by the loo package (Vehtari and Gelman, 2016). We will report results only for model 3, which performed best in the model selection (Appendix, Table 6). Model 3 includes an interaction term of experimental and adaptation temperature in the scaling of maximum feeding rate f, but not in the scaling of half-saturation density η. The fits of the full ODE together with the measured data points as well as functional response plots can be found in theAppendix (Appendix Figures 9 and 10). See Appendix also for full summary statistics, density plots and model code.

Table 3.1 – Models including experimental and adaptation temperature. All models include ln-linear terms of experimental temperature in the scaling of f, η, r, K (equations 3.4 - 3.7).

model	equations	terms for influence of adaptation temperature
1	3.4, 3.5	none
2	3.8, 3.9	ln-linear in f and η
3	3.10, 3.9	interaction with experimental temperature in f, ln-linear in η
4	3.8, 3.11	ln-linear in f, interaction with experimental temperature in η
5	3.10, 3.11	interaction with experimental temperature in f and η

Results

We found that over the course of 20 generations, predator body sizes decreased with increasing adaptation temperature, and thus predators adapted to higher temperatures had smaller average body sizes than predators kept at lower temperatures (Figure 3.3a). The half-saturation density (Figure 3.3b) generally increased with experimental temperature with no significant differences for predators adapted to different temperatures and a high variability (Table 3.2). According to the WAIC, model 3 (equations 3.10, 3.9) represented our data best, therefore, there was no interactive effect of experimental and adaptation temperature on half-saturation density. The effect of experimental temperature on half-saturation density equaled the activation energy $E_\eta = 4.359$ (with a standard deviation of 1.698 and a CI from 2.179 to 8.680) for predators adapted to all three adaptation temperatures. The effect of adaptation temperature on half-saturation density was slightly negative, but insignificant (Table 3.2). As half-saturation densities should not be affected by body size (Hansen *et al.*, 1997) the direct effect of adaptation equaled the realised effect (see Figure 3.2). Attack rates decreased with experimental temperature, with attack rates of cold adapted predators decreasing faster than attack rates of warm adapted temperature (Appendix Figure 15 and Tables 8, 9).

Table 3.2 – Mean values of the distribution and their standard deviation for normalisation constants of maximum feeding rate f_0 and half-saturation density η_0 and their activation energy main effects of experimental temperature E_f, E_η, of adaptive temperature A_f, A_η, and the interaction term for maximum feeding rate I_f. The range between 2.5 % and 97.5 % of the distribution give the 95 % credible intervals. For full summary statistic, please see Supporting Information Table 7.

	mean	sd	2.5 %	50 %	97.5 %
f_0	2.654	0.085	2.505	2.647	2.841
η_0	2378.247	1932.152	83.463	1930.298	7115.469
E_f	1.054	0.056	0.950	1.052	1.168
E_η	4.359	1.698	2.179	3.976	8.680
A_f	-0.362	0.053	-0.463	-0.364	-0.252
A_η	-0.530	0.627	-1.531	-0.617	0.860
I_f	0.569	0.122	0.380	0.548	0.855

In order to calculate the direct effect of adaptation on maximum feeding rates (Figure 3.2d), we factored body size into the respective maximum feeding rates, a posteriori to the per capita estimation of functional response parameters (equation 3.13 and 3.14). Investigating the direct effect of adaptation on maximum feeding rates revealed that warm adapted predators had highest maximum feeding rates at the highest experimental temperatures and lowest maximum feeding rates at the lowest experimental temperature (Figure 3.3c). Recent studies suggest a power law scaling of body size close to one for chemo-heterotrophic unicellular organisms yielding the same general results (Okie *et al.*, 2016) (results shown in Appendix, Figure 16). The physiological temperature adaptation was affecting activation energies. In predators adapted to 15° C, the activation energy for maximum feeding rate (equation 3.10) was approximately 0.66 and increased with adaptation temperature to approximately 1.05 and 1.43 for predators adapted to 20° C and 25° C, respectively (Table 3.3). In the realised adaptation scenario, maximum feeding rates (Figure 3.3d) generally increased with experimental temperature. Over most of the observed range of experimental temperatures, maximum feeding rate was highest for predators adapted to 15° C, followed by those adapted to 20° C, and lowest for those adapted to 25° C. Predators adapted to 25° C showed the steepest increase in maximum feeding rate with increasing experimental temperature, while predators adapted to 20° C and 15° C showed a shallower increase (Figure 3.3d). This resulted from a positive interaction between experimental and adaptation temperature (Table 3.1). However, at 25° C experimental temperature, there was no difference between maximum feeding rates of predators adapted to 15° C, 20° C or 25° C.

Table 3.3 – Median of estimated activation energies of maximum feeding rate (equation 3.12) for the ciliate predator *Tetrahymena pyriformis* adapted to 15° C, 20° C and 25° C for approximately 20 generations.

adaptation temperature	activation energy maximum feeding rate
15° C	0.663
20° C	1.054
25° C	1.431

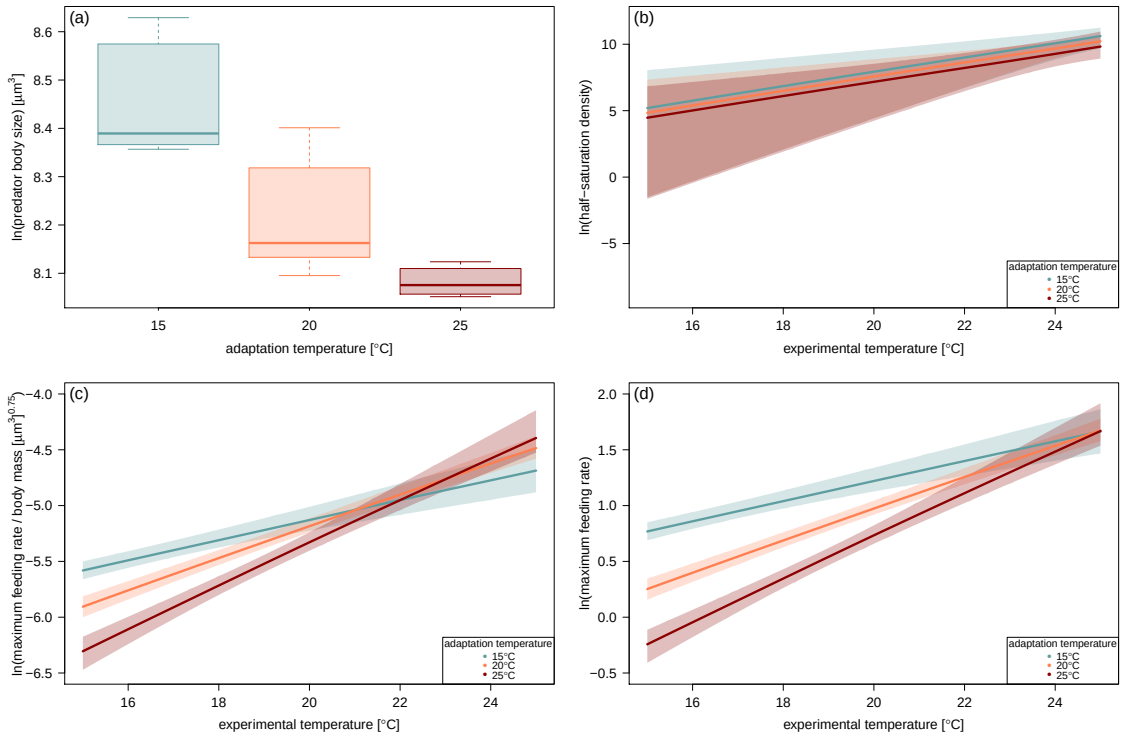

Figure 3.3 – **a) a) Body sizes** of *Tetrahymena pyriformis* adapted to 15° C, 20° C and 25° C in μm^3 measured in the Beckmann Coulter Counter decreased with adaptation temperature. **b) Half-saturation densities** for *Tetrahymena pyriformis* adapted to 15° C (blue), 20° C (orange) and 25° C (red) increased with experimental temperature. There was no significant difference for half-saturation density between predators adapted to different temperatures along the gradient of experimental temperatures. **c) Metabolic body-size accounted maximum feeding rates** ($f/body\ size\ 0.75\ [\mu m^3]$) for *Tetrahymena pyriformis* adapted to 15° C , 20° C and 25° C along an experimental temperature gradient showed an increase with experimental temperature while predators adapted to 15° C and 25° C showed the highest maximum feeding rates at their adaptation temperature, respectively. **d) Maximum feeding rates** for *Tetrahymena pyriformis* adapted to 15° C , 20° C and 25° C increased with experimental temperatures. While maximum feeding rates slightly decreased with adaptation temperatures, predators adapted to 25° C over 20 generations showed the strongest increase in maximum feeding with experimental temperature due to a positive interaction effect of experimental and adaptation temperature. Solid lines represent median values, shaded areas indicate 95 % credibility intervals.

Discussion

Increasing temperatures are putting a strain on biodiversity in ecosystems world wide. Previous studies have revealed an increasing mismatch between maximum feeding rates and metabolism with warming as an often overlooked and until recently poorly understood cause of extinction (Vucic-Pestic *et al.* 2011; Rall *et al.* 2012; Fussmann *et al.* 2014; Chapter 2).

Here, we investigated the effect of possible temperature adaptations on feeding interactions. After an adaptation period of approximately 20 generations, predator body size had decreased significantly for predators adapted to 25° C compared to predators kept at the lowest adaptation temperature according to our prediction based on previous studies (Bergmann, 1847; Daufresne *et al.*, 2009; Yvon-Durocher *et al.*, 2011). We ran functional response experiments along a temperature gradient with predators adapted to different temperature regimes and found that experimental temperature has an effect on half-saturation densities of predators adapted to all three adaptation temperatures (Fussmann *et al.* 2014; Chapter 2). Using more than one predator per experimental treatment, the particularly high values of half-saturation densities might be explained by predator interference. Interference has been observed among unicellular organisms (Curds and Cockburn, 1968) and can be affected by temperature changes (Lang *et al.*, 2012). By reducing the time available for prey encounters, interference lowers the feeding efficiency of predators (Abrams and Ginzburg, 2000). In cases where half-saturation density and interference both increase with warming, this could lead to a combined effect on half-saturation densities. Declining attack rates with experimental temperature can be caused by increasing interference and therefore corroborate this assumption. However, since we did not vary predator density to manipulate the strength of predator interference, this can only be speculated. According to our model comparison there is no interactive effect of experimental and adaptation temperature on half-saturation density. This suggests, that the effect of adaptation temperature on half-saturation-density is buffered by a simultaneous temperature adaptation of attack rate and maximum feeding rate. Therefore, adaptation of half-saturation densities should be excluded as a possible mechanism to counteract temperature effects on carrying capacities and decreasing prey abundances at higher temperatures in natural systems. However, predators adapted to higher temperatures show the steepest increase of maximum feeding rate with increasing experimental temperature enabling them to react to increasing temperatures quicker and increase their energy intake faster within the measured temperature range. Predators adapted to 25° C show lower maximum feeding rates at 15° C and 20° C than cold adapted predators, while at 25° C experimental temperature, all predators show similar maximum feeding rates. In our experiment we were unable to document potential changes in metabolism for predators

adapted to different adaptation temperatures, which leaves two possible hypotheses to explain our findings. The hypothesis that metabolic rates were unaffected by adaptation temperature leads to the conclusion that predators adapted to higher temperatures have gained a disadvantage at lower experimental temperatures becoming less efficient compared to their cold adapted counterparts, while there is no clear advantage gained at high experimental temperatures. However, due to smaller body sizes of warm adapted predators, predators adapted to 25° C adaptation temperature are expected to have lower metabolic demands compared to cold adapted predators, if any potential physiological adaptation of metabolism is taken into account (Brown *et al.*, 2004). Relevantly, our experimental units contained more than one predator individual, these lowered metabolic demands can lead to an increase in predator interference, reducing maximum feeding rates at low experimental temperatures. With increasing experimental temperatures, these predators will prioritise feeding over predator interaction leading to the strong increase of maximum feeding rates with experimental temperature in warm adapted predators. While some studies predict activation energies for maximum feeding rates ranging from 0.6-0.7 eV, our results are in the range of activation energies reported for ciliated protozoan and other unicellular organisms around 0.772 eV (Hansen *et al.*, 1997; Vasseur and McCann, 2005). Activation energies for metabolism drawn from respiration measurements by Laybourn & Finlay (1976) of 0.96 eV (Fussmann *et al.* 2014; Chapter 2), match the range of activation energies of maximum feeding rates in our functional response measurement. Predators adapted to 20° C and 25° C show higher activation energies to counteract increasing metabolic demands at higher temperatures. Combining the strong increase in maximum feeding rate with the change in intercept caused by body size adaptation, these results are in line with the hypothesised interactive effect of body size adaptation, and adaptation temperature and experimental warming on maximum feeding rates.

Over the timespan of 20 generations, our results as well as previous studies have shown that adaptation to increased temperatures influences protist body sizes (Atkinson *et al.*, 2003) highlighting the importance of trans-generational studies regarding not only genetic adaptation but also phenotypic changes (DeLong *et al.*, 2016). Larger species, predominantly found at higher trophic levels (Riede *et al.*, 2011) are most vulnerable to extinction due to an energetic mismatch with increasing temperatures (Binzer *et al.*, 2012). This leads to a shift towards smaller species in aquatic systems (Daufresne *et al.*, 2009; Yvon-Durocher *et al.*, 2011). The relationship between increasing predator body size and maximum feeding rate follows a 3/4 power-law scaling (Hansen *et al.*, 1997; Rall *et al.*, 2012), leading to lower maximum feeding rates in smaller predators. To disentangle the indirect effect of predator body size on the realised maximum feeding rate from the direct effect of physiological adaptation we corrected our results accordingly (see Figure 3.2 and equations 3.13 and 3.14 for a detailed derivation). Once this change in body size is accounted for,

we found that at 25° C experimental temperature, maximum feeding rates shift towards a scenario that suggests a specialised temperature adaptation of predators. While at 15° C predators adapted to that temperature show the highest maximum feeding rates, at 25° C predators adapted to 25° C show the highest maximum feeding rates. There is not one culture adapted to have the best fitness at the full temperature range, rather predators seemed to be adapted to their respective temperature. The direct physiological adaptation of maximum feeding rates leads to a stronger increase in maximum feeding rate with experimental temperature in warm adapted predators. Further, in form of a morphological adaptation to warming, with a smaller average body size, predators increase per-biomass consumption while reducing metabolic demand. This increases the effect of physiological adaptation of maximum feeding rates, resulting in a combined effect increasing overall energy efficiency in warm adapted predators at high temperatures.

In conclusion, our results suggest that while un-adapted predators face a mismatch between maximum feeding rates and metabolic demands with increasing temperatures leading to starvation and extinction of predators, adaptation poses a viable escape from this scenario. By decreasing their body size over the course of 20 generations at higher temperatures, predators lower their per-capita metabolic rates. Therefore, the ratio between metabolic costs and maximum feeding rates increases for warm adapted predators, decreasing their risk of starvation. The decrease in the risk of starvation also implies a decreased risk of extinction which may buffer expected biodiversity loss with climate warming and increased ecosystem stability. It is widely accepted that adaptation occurs within ecological time spans and is, therefore, of utmost importance for the understanding of population stability and ecosystem dynamics under the threat of an increasingly fast changing environment (Holt, 1990; Lynch and Lande, 1993; Burger and Lynch, 1995; Merilä, 2012; Merilä and Hendry, 2014). Especially in a homogeneous environment like water, where stressors cannot be avoided by migration or refuge in microhabitats, the strain of climate change poses a particularly high risk for populations (Bergmann *et al.*, 2010). Adaptation might be a possible way for populations to deal with increasing temperatures and persist in a warming environment.

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Chapter 4.

Temperature adaptation of predator interference

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Abstract

Global warming is threatening predators on higher trophic levels through temperature induced mismatches of energy intake (feeding) and use (metabolism) with severe effects on population stability. While previous studies focussed on the effects of temperature on prey density dependent feeding rates, the effects of temperature adaptation on predator interference remain unknown. Here, we designed microcosm experiments with the ciliated protozoan *Tetrahymena pyriformis* preying on the bacterium *Pseudomonas fluorescens* to observe the effects of experimental temperature and temperature adaptation of *T. pyriformis* after approximately 20 generations on the functional response parameters attack rate, handling time and predator interference. Attack rates increased with experimental temperature with the steepest increase in cold-adapted predators. Handling times decreased for predators adapted to all adaptation temperatures with generally higher rates and the steepest decreases with experimental temperature in warm adapted predators. Predator interference increased with experimental temperature for all adapted predators with the overall highest rates and the most shallow increase for warm adapted predators. Our results suggest that temperature adaptation to warmer temperatures has a stabilising effect by increasing net energy gain and enabling higher levels of predator interference. However, reduced body sizes and lower maximum feeding rates potentially limit the energy flow through food webs, mechanistically explaining the occurrence of smaller species, fewer links and lower trophic levels under warming.

Introduction

Climate change is progressing fast, the IPCC report predicts an increase in average surface temperature of 1.5° C until the end of this century (IPCC, 2014) and the associated decline in biodiversity is potentially much greater than previously suggested (Pereira *et al.*, 2010).

Interaction strengths between different species play a vital role in the stability of ecosystems (McCann, 2000) and temperature alters feeding interactions by determining the speed of their underlying biological reactions (Brown *et al.*, 2004). Since the impact of temperature is not synchronous for all rates, this can create mismatches destabilising species (Vucic-Pestic *et al.* 2011; Fussmann *et al.* 2014; Chapter 2) and potentially cause extinction (Cahill *et al.* 2012; Fussmann *et al.* 2014; Chapter 2). In cases where feeding increases stronger with warming than metabolic demands of the predator, predator-prey systems are destabilised and oscillate strongly in their abundance (Vasseur and McCann 2005; Fussmann *et al.* 2014; Chapter 2), eventually leading to extinctions (Rosenzweig, 1971). In cases where metabolic demands increase faster than feeding, population dynamics get dampened, eventually leading to the extinction of the predator (Binzer *et al.* 2012; Fussmann *et al.* 2014, Chapter 2).

Functional responses are an established tool to describe feeding interactions and, therefore, species interaction strengths (Holling, 1959*b*). In the hyperbolic Holling type II functional response (from here on type 2), attack rate, the rate of a predator's successful search for prey and capture, determines the initial increase of functional responses at low prey densities (Holling 1959*b*, Figure 4.1a). Handling time, the time needed to kill, eat and digest prey organisms, defines maximum feeding rates and functional responses at high prey densities (Holling 1966; Jeschke *et al.* 2002; Koen-Alonso 2007, Figure 4.1a).

The Holling type III functional response (from here on type 3) is characterised by a sigmoid shape induced by a prey density dependent attack rate (Figure 4.1b). Biologically, type 3 functional responses describe systems with prey refuges (Scheffer and De Boer, 1995; Vucic-Pestic *et al.*, 2010), prey switching (Murdoch, 1969) or learning behaviour (Holling, 1966). Type 2 and type 3 functional responses only account for the influence of prey abundance on feeding interactions, independent of predator abundance. However, predator interference is common in natural systems (Abrams and Ginzburg, 2000; Skalski and Gilliam, 2001; Ginzburg and Jensen, 2008) and potentially a major force shaping evolutionary and ecological processes (Gause, 1934). Over the past centuries, different approaches have been developed to describe predator interference in functional responses (Jeschke and Tollrian, 2000; Skalski and Gilliam, 2001) and two well-established mechanistic interference models are the Beddington-DeAngelis functional response (Beddington, 1975; DeAngelis *et al.*, 1975) and the Crowley-Martin functional response (Crowley and Martin, 1989). While in the Beddington-DeAngelis functional response, interference becomes negligible at high prey

density and feeding and interaction are two entirely exclusive processes (Figure 4.1c, d), the Crowley-Martin functional response accounts for predator interference even at high prey densities allowing for different asymptotic feeding rates at different predator abundances (Figure 4.1e, f).

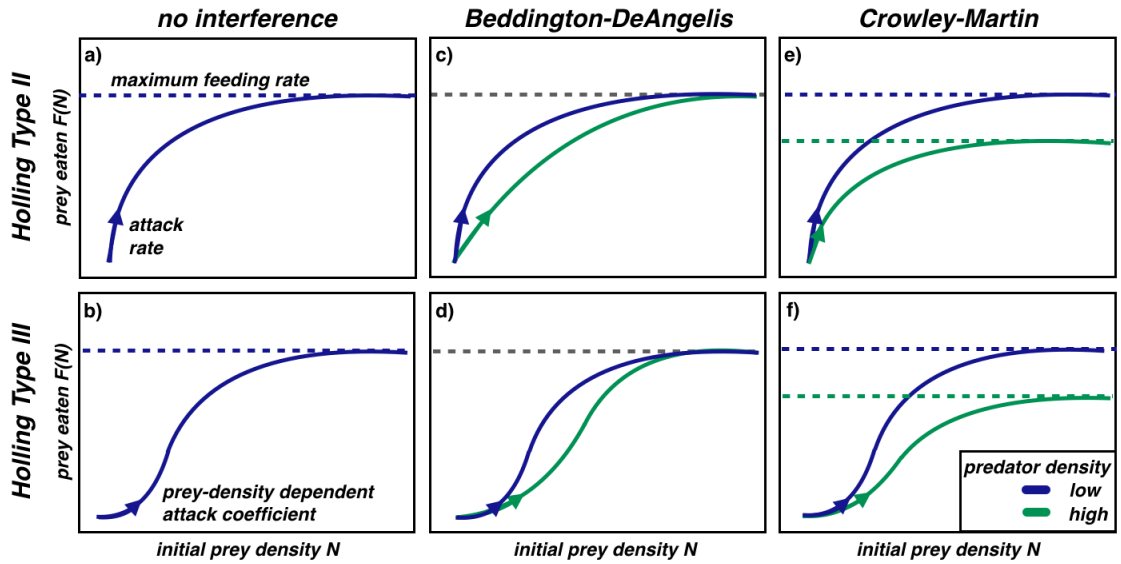

Figure 4.1 – Prey-dependent and prey- and predator-dependent functional response models: **a) Holling type 2 functional response** characterised by maximum feeding rate (dashed line) which can be described as the inverse of handling time and the attack rate (arrow), characterising the slope at low prey densities. **b) Holling type 3 functional response** which is, apart from maximum feeding rate, characterised by a prey density dependent attack rate (arrow). **c) Beddington-DeAngelis type 2 functional response**: with increasing predator abundance, attack rates decrease while maximum feeding rate remains unaffected. Low predator densities are displayed in blue, high predator densities are displayed in green. **d) Beddington-DeAngelis type 3 functional response**: with increasing interference attack rates decrease while interference does not affect maximum feeding rates at high prey densities. **e) Crowley-Martin type 2 functional response**: Attack rates and maximum feeding rates decrease with increasing predator interference **f) Crowley-Martin type 3 functional response**: Maximum feeding rates and attack rates decrease with increasing predator interference.

Biochemical reactions increase with increasing temperature and with them all dependent biological rates (Brown *et al.*, 2004). This includes swimming speed, affecting the volume a predator can explore and the encounter rate with prey, both driving attack rates (Dell *et al.*, 2014). The underlying biochemical reactions are determining the speed of digestion increase with increasing temperatures, leading to shorter handling times (Thompson, 1978) and subsequently increasing maximum feeding rates (Rall *et al.*, 2012). This increase of attack rates and maximum feeding rate counteracts metabolic demands which also increase with warming (Brown *et al.*, 2004). Predator interference depends on the number of encounters with other predators and the time spent on each encounter (Lang *et al.*, 2012). Due to increased encounters with warming, interference should increase (Dreisig, 1981; Kruse *et al.*,

2008). However, the time spent on encounters is hard to predict, with the potential to increase or counteract the encounter driven increase of interference (Lang *et al.*, 2012). In cases where feeding increases faster with temperature than metabolic demands, predators are likely to increase the time spent interacting with other predators (Lang *et al.*, 2012), subsequently leading to an increase of predator interference with warming. In cases where metabolic demands increase faster with temperature than feeding, predators might spend less time on interactions with other predators, decreasing the overall interference (Lang *et al.*, 2012).

Adaptation to environmental temperature can occur within biological time frames and alter ecological dynamics (Lynch and Lande, 1993; Merilä and Hendry, 2014). While the impact of temperature adaptation of different functional response parameters has been documented in different species and over different time frames (Sentis *et al.* 2015; Chapter 3), the possible adaptation of predator interference remains unknown.

Adaptation to temperature can be a direct adaptation of physiological rates, or an indirect effect on biological rates via adaptation of body size of the organisms. The body size of organisms decreases with warming (Bergmann 1847; Yvon-Durocher *et al.* 2011; Chapter 3, Figure 4.2a). A decrease in body size decreases metabolic demands (Brown *et al.*, 2004) consequently leading to decreased attack rates (Figure 4.2b) and increased handling times (Rall *et al.* 2012; Pawar *et al.* 2012, Figure 4.2c). Interference should decrease with decreasing body size through the lower number of encounters with other predators (Wissinger and McGrady, 1993; Lang *et al.*, 2012) but a recent meta-study revealed that it remains highly variable with a potentially mitigating, neutral effect (DeLong, 2014). Apart from body size adaptation to increasing temperatures, predators are potentially able to adapt biological rates physiologically to optimise their energy gain and cope with rising temperatures (Padfield *et al.* 2015; Sentis *et al.* 2015; Chapter 3). Under the assumption that cold and heat tolerance are genetically independent, this would implicate a widening of the temperature performance curve (Hoffmann and Parsons, 1989; Huey and Kingsolver, 1993). This can potentially affect metabolic rates leading to lower metabolic demands (Padfield *et al.*, 2015) as well as parameters determining energy intake (Sentis *et al.*, 2015) leading to an increased energy gain for warm-adapted predators (Figure 4.2e). This puts cold adapted predators under higher energetic stress with increasing experimental temperature. Time that is spent on predator-interaction at low experimental temperatures will be facilitated to launch prey attacks at higher experimental temperatures to cover the faster increasing energetic demands. Therefore, attack rates are expected to increase faster with experimental temperature in cold-adapted predators than attack rates in warm adapted predators (Sentis *et al.* 2015, Figure 4.2f). Predators adapted to warmer temperatures will physiologically improve maximum feeding rates by reducing handling time (Sentis *et al.* 2015; Chapter 3). Predators adapted to higher temperatures

will have lower handling times than cold-adapted predators at high temperatures with a steeper decrease to shorten handling times (Chapter 3, Figure 4.2g). While predators adapted to warmer temperatures will be physiologically more energy efficient, the time spent on predator interactions on the expense of feeding interactions will be higher than in cold-adapted predators within the range of biologically relevant temperatures. However, predator interference will increase fast with experimental temperature in cold adapted predators through faster increasing swimming speed and higher encounter rates (Figure 4.2h).

Here, we designed microcosm experiments for conducting functional response experiments at three experimental temperatures (15° C, 20° C and 25° C) and four different predator densities with predators adapted to three adaptation temperatures (15° C, 20° C and 25° C) for approximately 20 generations to investigate the interplay between temperature adaptation of feeding rates, body size and predator interference. (1) Through body size as well as physiological adaptation, we expect an increase in attack rates with experimental temperature through increased swimming speed. While we expect attack rates to increase faster with experimental temperature in predators adapted to lower temperatures, attack rates will be higher for cold-adapted predators in the temperature range of our experiment (Figure 4.2i). (2) We expect handling times to decrease with experimental temperature, with a steeper decrease for warm adapted predators. The effect of body size adaptation and physiological temperature adaptation should result in lower handling times for cold-adapted predators with bigger body sizes (Figure 4.2h). (3) We expect interference to increase with increasing experimental temperature with a steeper increase in cold-adapted predators and a higher level of interference in warm-adapted predators (Figure 4.2k).

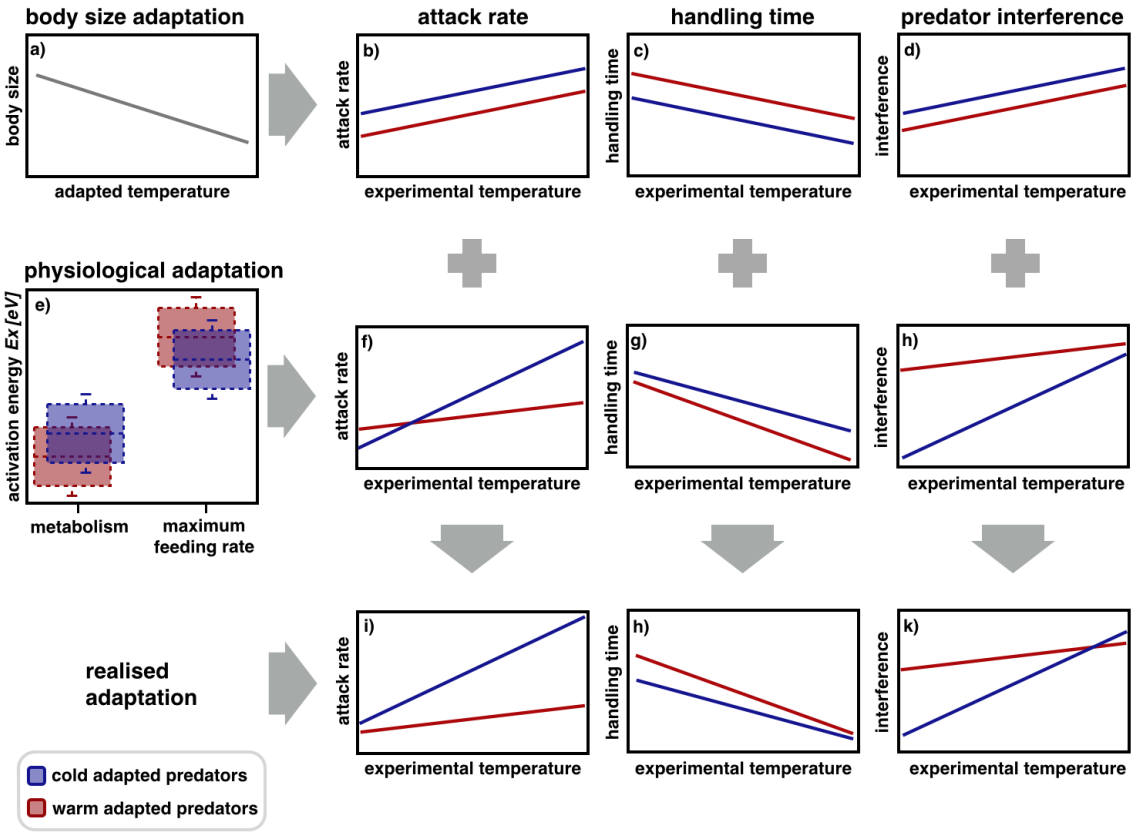

Figure 4.2 – **Temperature adaptation of functional response and interference parameters. a) body size adaptation**: Organisms adapted to higher temperatures have been shown to develop smaller body sizes. **b) Attack rates** increase with experimental temperature but are smaller in warm-adapted, smaller predators (red) due to decrease swimming speed. **c) Handling times** decrease with increasing temperatures but are higher in smaller predators due to an increased prey-predator body size ratio. **d) Interference** is tendentiously lower for smaller predators through decreased number of encounters but remains highly variable through unpredictable impacts of body size on the time spent on predator encounters. **e) The impact of physiological adaptation of functional response and interference parameters** depends on the interplay between the activation energies of metabolism and maximum feeding rates. Warm-adapted, small predators have lower metabolic demands compared to bigger, cold-adapted predators (blue). While maximum feeding rates are generally lower in smaller predators, warm-adapted predators might potentially increase the activation energy of their maximum feeding rates to increase energy gain. **f) Attack rates** of cold-adapted predators will increase faster with experimental temperature based on the assumption, that time invested in predator interference at cold experimental temperatures is freed under rising experimental temperatures and high energetic demands and invested in launching attacks on prey. **g) Handling times** are likely to decrease faster for warm-adapted predators compared to predators adapted to lower adaptation temperatures with a faster digestion to increase maximum feeding rates. **h) Interference** in warm-adapted predators will be higher and the increase with temperature shallower, since their higher energy gain will allow more time for predator interference than in cold-adapted predators where the priority lies on feeding. **i) Attack rates** will be higher for cold adapted predators due to body size adaptation and we expect a faster increase with experimental temperature in predators adapted to lower temperatures. **h) Handling times** of cold-adapted predators will be lowered through body size adaptation and decrease more slowly with experimental temperature than for warm adapted predators. **k) Interference** will be higher in warm-adapted predators but increase faster with experimental temperature in cold-adapted predators.

Methods

Laboratory methods

Microcosm experiments were conducted in a microbial predator-prey system with the ciliated protozoan *Tetrahymena pyriformis* CCAP 1630/1W (CCAP Culture Collection of Algae and Protozoa, SAMS Limited, Scottish Marine Institute, Scotland, United Kingdom) preying on the fluorescent marked bacterial strain *Pseudomonas fluorescens* CHA19-gfp (Haas *et al.*, 2002; Zuber *et al.*, 2003; Weller *et al.*, 2007). For every run of functional response experiments, transformed bacteria stored at -80° C were unfrozen and plated on agar plates containing 8 mg gentamycin before a single colony was incubated in liquid LB-media at room temperature over night. Prior to the experiment, bacterial cells were transferred into sugarless sterile Volvic by centrifuging at 13.000 rpm for 1 minute and re-suspending in Volvic three times. To minimise bacterial growth during experiments, bacteria were stored in Volvic for two hours before the experiment.

Tetrahymena pyriformis was cultured in 250 ml cell culture flasks in 2 % proteose peptone media (Altermatt *et al.*, 2015). At the beginning of the adaptation experiment, one culture, previously incubated at 20° C, was split into nine subcultures, three of which were to be incubated at 15° C, 20° C and 25° C, respectively, for approximately 20 generations (Chapter 3). 24 hours before the experiment, protists were transferred into sugarless media (Volvic) by gentle centrifugation at 300 rpm for 7 minutes at 0° C and resuspension in sterilised Volvic three times. Cells were starved for 12 hours at their respective adaptation temperature prior to functional response experiments. Cell densities were measured in a Beckman Coulter Counter T4 with a 100 μm aperture on slow fluidics speed (Beckman Coulter, Inc.), samples were diluted in Isoton 1:100.

Functional response experiments with a volume of 200 μl were conducted in 96 well plates. Each plate contained 11 different prey start densities ranging from 26938 to 1126767 $[\mu l^{-1}]$ and one blank containing only the predator *Tetrahymena pyriformis*. Further, each experiment was replicated 6 times with two additional control treatments containing only the prey *Pseudomonas fluorescens*, per plate. This experimental setup ran for 4 different predator densities, 50, 100, 200 and 400 predators $[\mu l^{-1}]$ at three different experimental temperatures 15° C, 20° C and 25° C for each predator culture adapted to 15° C, 20° C and 25° C. Different predator densities were replicated on different plates. Experiments ran for 8 hours with one measurement per hour, the first 4 hours were excluded from the analysis due to transient dynamics. Measurements were taken with a Tecan plate reader infinite M200 (Tecan Trading AG, Switzerland) measuring the green fluorescent signal of bacterial prey after orbital shaking for 10 seconds. Each well was measured with an excitation wavelength of 485 nm and an emission wavelength of 520 nm reading 15 flashes with a manual gain of

100. The gfp signal (green fluorescent protein) was transferred into bacterial counts with the help of comparative measurements with an accuri C6 flow cytometer (BD Biosciences, Becton, Dickinson and Company) on slow with an FSC-H of 8000 and an SSC-H of 2000 (Chapter 3). In total, we analysed 731 control treatments without predators and 1353 time-series containing 4 different predator densities (for exact numbers of treatments, please see Appendix Table 5). Each time-series consists of 5 measurements taken after 4, 5, 6, 7 and 8 hours into the experiment.

Functional responses

Bacterial growth and death, G, in control treatments were accounted for with the Gompertz growth model for microbial systems (equation 4.1, Gompertz 1825; Paine *et al.* 2012).

$$G = rNln\frac{K}{N} \tag{4.1}$$

Without a predator present, changes in prey density N depend on the intrinsic growth rate r and the carrying capacity of the population K.

The functional response analysis is based on Holling's classic models, where feeding F can be described by the classic Holling type 2 functional response:

$$F = \frac{aN}{1 + ahN} \ , \tag{4.2}$$

where a is the attack rate and the handling time h can be described as $h = 1/f$. Describing the sigmoid shape of the type 3 functional response is parameter b:

$$F = \frac{bN^2}{1 + bhN^2} \ , \tag{4.3}$$

note that the attack rate $a = bN$ is prey density dependent in the type 3 functional response. To incorporate the interference parameter c, we compared the Beddington-DeAngelis model as type 2 functional response (equation 4.4a) and type 3 functional response (equation 4.5b)

$$F = \frac{aN}{1 + ahN + c(P - P_{min}} \ , \tag{4.4}$$

$$F = \frac{bN^2}{1 + bhN^2 + c(P - P_{min}} \ , \tag{4.5}$$

and the Crowley-Martin model as type 2 (equation 4.6a) and type 3 (equation 4.7b) functional response:

$$F = \frac{aN}{1 + ahN + c(P - P_{min} + ahNc(P - P_{min}} \ , \tag{4.6}$$

$$F = \frac{bN^2}{1 + bhN^2 + c(P - P_{min} + bhN^2c(P - P_{min}} \ . \tag{4.7}$$

P is the predator density, P_{min} is the lowest predator abundance used for experiments in this study. These standard models to estimate feeding interactions are solved as ordinary differential equations (ODE) extended by the Gompertz growth in order to account for prey growth and death, not only in control treatments but also predator treatments:

$$\frac{dN}{dt} = G - FP \ . \tag{4.8}$$

We used an exponential temperature dependency of the growth parameters r and K:

$$x = x_0 \ e^{E_x \frac{(T_e - T_0)}{kT_e - T_0}} \ , \tag{4.9}$$

where x_0 is a parameter's normalisation constant and E_x its experimental activation energy (Arrhenius, 1889; Gillooly *et al.*, 2001). T_e $[K]$ is the absolute experimental temperature, T_0 $[K]$ is the normalisation temperature and k $[eVK^{-1}]$ is the Boltzmann's constant. For the functional response parameters a, h, and b and the interference coefficient c we additionally accounted for effects of adaptation temperature on the functional response parameters and calculated activation energies for adaptation temperature A_x for attack rate A_a, attack coefficient A_b and handling time A_h and the interference coefficient. The interaction effect of experimental and adaptation temperature is expressed in the interactive activation energy I_x:

$$x = x_0 \ e^{E_x \frac{(T_e - T_0)}{kT_e - T_0}} \ e^{A_x \frac{(T_a - T_0)}{kT_a - T_0}} \ e^{I_x \frac{(T_e - T_0)}{kT_e - T_0} \ \frac{(T_a - T_0)}{kT_a - T_0}} \ . \tag{4.10}$$

This exponential framework is generally used to describe temperature effects on functional response parameters (Brown *et al.*, 2004; Savage *et al.*, 2004; Vucic-Pestic *et al.*, 2011; Rall *et al.*, 2012; Binzer *et al.*, 2016) and evolutionary rates (Gillooly *et al.*, 2005). Here, we use it to test our data for an interactive effect of adaptation and experimental temperature. Further, we calculated realised activation energies $\tilde{E}_x$ for attack rate, attack coefficient, maximum feeding rate and predator interference for predators adapted to

different adaptation temperatures.

$$\tilde{E}_x = E_x + I_x \frac{(T_a - T_0)}{kT_a - T_0} \tag{4.11}$$

Fitting algorithm and model comparison

We used Bayesian methods for fitting the dynamical models. Model parameters for control treatments (equation 4.1 including the scaling relationships in equation 4.9) were estimated separately from treatments with predators present (equations 4.2, 4.3, 4.4, 4.5, 4.6, 4.7) including the scaling relationships of equations 4.10). Data of prey densities after 4 hours $N(t4)$ were used as initial values, excluding the first 4 hours of the experiments as transient dynamics, for the numerical solution of the ordinary differential equations (ODE) and data of densities after 5, 6, 7 and 8 hours $N(t5), ..., N(t8)$ were modelled using ln-normally distributed errors. All normalisation constants (r_0, K_0, a_0, b_0, h_0, c_0) were estimated on ln-scale. Samples from the posterior distribution of the parameters given the data were drawn using Hamiltonian Monte Carlo sampling in Stan, accessed via the RStan package (Stan Development Team, 2016). The Stan software comes with a built-in ODE-solver, making it suitable for fitting ODE-based functional responses. We used normally distributed uninformative priors with zero means and standard deviations of 100 for all model parameters and a uniform distribution on the interval between 0 and 100 as a prior for the model's standard error. We ran 5 Markov chains in parallel with an adaptation phase of 1,000 iterations and 2,000 sampling iterations each, summing up to 10,000 samples of the posterior distribution. Visual inspection of the trace plots and density plots showed a good mixture of the chains, values of $\grave{R}$ sufficiently close to 1 and an adequate, effective sample mass n_{eff} further verified convergence (Appendix, Tables 12-17). See Supporting Information for full summary statistics, density plots and model code. For model comparison, we used the Watanabe-Akaike information criterion (WAIC), which can be computed from the log-likelihood values of the posterior samples by the loo package (Vehtari and Gelman, 2016).

Results

We initially tested all possible model combinations of type 2, and type 3 functional responses without interference, Beddington-DeAngelis interference as type 2 and type 3 and Crowley-Martin interference as type 2 and type 3 functional response. According to the WAIC, the best model describing our data was the type 3 Crowley-Martin functional response (Table 4.1, Figure 4.3).

Table 4.1 – WAIC scores (Watanabe-Akaike information criterion, smallest indicates the best model) and their standard errors. Further, direct comparison of differences in out-of-sample predictive accuracy ($elpd = -0.5 * WAIC$) to the type 3 Crowley-Martin functional response model and their standard errors.

model	WAIC	se_{WAIC}	$elpd_{diff}$	$se_{elpd_{diff}}$
Crowley-Martin type 3	-2181.2	172.3		
Beddington-DeAngelis type 2	-1894.4	177.8	-143.4	28.8
Crowley-Martin type 2	-1837.2	173.6	-172.0	19.5
Beddington-DeAngelis type 3	-1068.1	185.2	-556.5	52.0
Holling type 3	2013.7	188.7	-2097.5	66.4
Holling type 2	2035.9	188.8	-2108.6	72.0

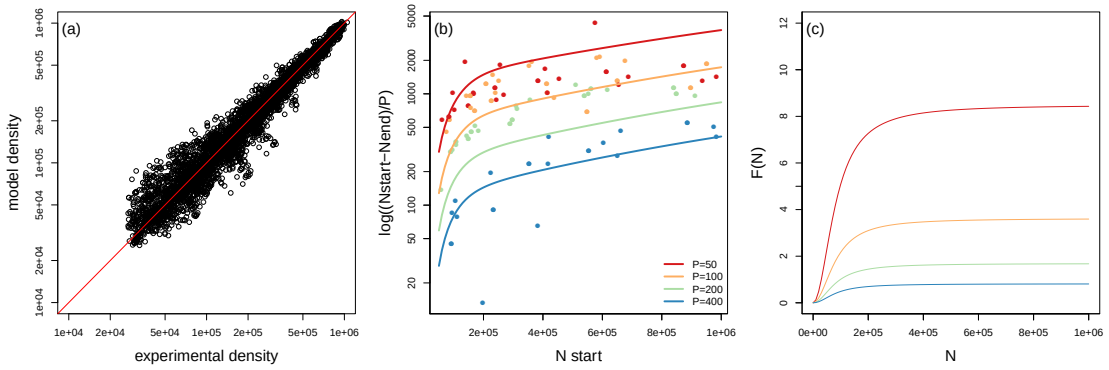

Figure 4.3 – a) Empirical prey densities compared to predicted prey densities of the Crowley-Martin type 3 ODE for all functional response treatments. **b) Crowley-Martin type 3 ordinary differential model** (lines) and experimental data (points) of bacterial densities for treatments containing 50 predators μl^{-1} (red), 100 predators μl^{-1} (yellow), 200 predators μl^{-1} (green) and 400 predators μl^{-1} (blue). Displayed here is the graph for predators adapted to 20° C adaptation temperature at feeding at 20° C experimental temperature (see Appendix Figure 23 for other temperatures). **c) Functional response graphs of the Crowley-Martin type 3 functional response** (equation 5b) for predators adapted to 20° C adaptation temperature at feeding at 20° C experimental temperature (see Appendix Figure 24 for other temperatures).

Attack coefficients showed a significant positive interaction of adaptation temperature and experimental temperature (Table 4.2, Figure 4.4a). Attack rates increased with experimental temperature for predators adapted to 15° C, 20° C and 25° C adaptation temperature. At the lowest experimental temperature, all predators showed similar attack coefficients. Predators adapted to 15° C show the steepest increase with experimental temperature with an activation energy of 1.365 eV (equation 3.9), while our results showed an activation energy of 0.960 eV for predators adapted to 20° C. Predators adapted to the highest adaptation temperature of 25° C showed the shallowest increase of attack coefficient with experimental temperature resulting in an activation energy of 0.568 eV.

Adaptation to temperature and experimental temperature showed a significant, negative interaction term for handling time (Table 4.2, Figure 4.4b). For all adaptation temperatures, handling times decreased with increasing experimental temperature whereas activation energies were lowest for predators adapted to 15° C with an activation energy of -0.650 eV (equation 4.11) showing the shallowest decrease in handling time with experimental temperature, and slightly increased with adaptation temperature for predators adapted to 20° C to -0.761 eV. Predators adapted to 25° C adaptation temperature had the steepest decrease in handling time with experimental temperature with an activation energy of -0.868 eV. This results in increasing maximum feeding rates with experimental temperature with the steepest increase in warm adapted predators and similar maximum feeding rates at the highest experimental temperature 25° C for predators adapted to all three adaptation temperatures (Appendix, Figure 25). As a result of attack rates and maximum feeding rates, half-saturation densities decrease with experimental temperature for predators adapted to 15° C and 20° C and increase with experimental temperature for predators adapted to 25° C (Appendix, Figure 26).

Our results showed a significant negative interaction of experimental and adaptation temperature for predator interference (Table 4.2, Figure 4.4c). While at 25° C experimental temperature, predators adapted to all three adaptation temperatures showed similar rates of predator interference, predators adapted to 15° C adaptation temperature showed the lowest levels of predator interference with the steepest increase with experimental temperature resulting in an activation energy of 1.423 eV (equation 10). While predators adapted to 20° C had an activation energy for predator interference of 1.001 eV, predators adapted to 25° C had the shallowest increase of interference with experimental temperature and an activation energy of 0.592 eV.

Table 4.2 – Mean and standard deviations for parameters of attack coefficient b, handling time h and interference coefficient c as predicted by the Crowley-Martin type 3 ordinary differential equation model (equation 4.7). 95 % credible intervals correspond to the 2.5 % and 97.5 % quantiles of the posterior distribution. For the full summary output, please see Appendix Table 17 and Table 12-16 for the summary output of the other models.

	mean	sd	2.5%	50%	97.5%
$ln(b_0)$	-20.487	0.041	-20.569	-20.487	-20.405
E_b	0.960	0.081	0.080	0.959	1.119
A_b	-0.414	0.071	-0.553	-0.415	-0.277
I_b	-0.590	0.134	-0.853	-0.592	-0.328
$ln(h_0)$	-2.138	0.024	-2.185	-2.139	-2.092
E_h	-0.761	0.043	-0.846	-0.761	-0.668
A_h	0.267	0.039	0.192	0.268	0.345
I_h	-0.161	0.070	-0.297	-0.161	-0.023
$ln(c_0)$	-3.615	0.029	-3.672	-3.615	-3.558
E_c	1.001	0.054	0.895	1.000	1.111
A_c	0.346	0.048	0.253	0.347	0.439
I_c	-0.615	0.088	-0.788	-0.616	-0.442

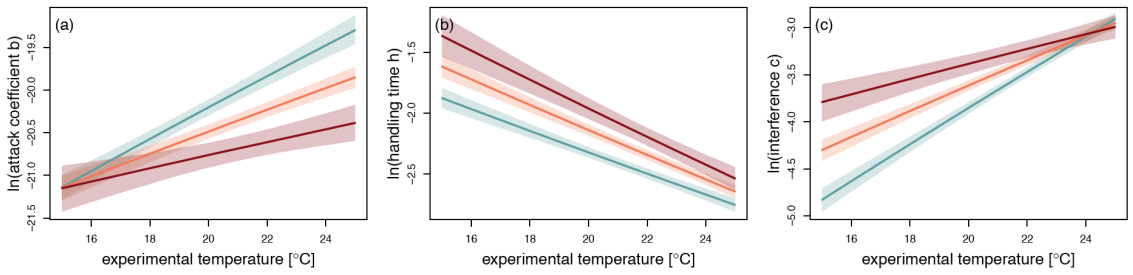

Figure 4.4 – a) Attack coefficient b, for 50 predators μl^{-1} increases with experimental temperature for predators adapted to all 3 adaptation temperatures. Predators adapted to 15° C (blue) show a steeper increase with experimental temperature than predators adapted to 20° C (orange) with the shallowest increase for predators adapted to 25° C (red). At 15° C experimental temperature all predators have similar attack coefficients. **b) Handling time** h decreases with experimental temperature for predators adapted to all adaptation temperatures. Predators adapted to 25° C show higher handling times and the steepest decrease with experimental temperature compared to predators adapted to 20° C with the lowest handling times for predators adapted to 15° C. **c) Predator interference** c increases with experimental temperature for predators adapted to all three adaptation temperatures. Predators adapted to 25° C have the highest levels of predator interference with the shallowest increase with experimental temperature. At 25° C experimental temperature, predators adapted to all three adaptation temperatures show similar levels of interference. Lines represent the median values, shaded areas represent 95 % credible intervals.

Discussion

Interaction strengths of predator-prey feeding interactions have become an important predictor of ecosystem stability in a quickly changing environment (May, 1972; McCann, 2000; Brose *et al.*, 2006; Rall *et al.*, 2010). Here we not only investigated the impact of experimental temperature on attack rates, handling times and predator interference but also temperature adaptation of those rates after approximately 20 generations to draw conclusions about its potential effect on predator-prey interactions.

Our data was best described by the Crowley-Martin type 3 functional response (Crowley and Martin, 1989; Lang *et al.*, 2012). At low prey densities, feeding interactions are characterised by attack coefficients which in our experiment increased with experimental temperature because temperature increases the swimming speed of predators (Dreisig, 1981; Kruse *et al.*, 2008). Faster swimming allows predators to widen their search area and increase encounter rates. Body mass also increases swimming speed leading to higher attack coefficients in cold-adapted, bigger predators compared to smaller, warm-adapted predators. The time available for attacks on prey is potentially limited by time spent interacting with predators (Abrams and Ginzburg, 2000). In cold-adapted predators, attack coefficients show a faster increase with experimental temperature than in warm adapted predators. Under the assumption that they are less energy efficient and their energy gain is lower, with increasing temperatures, they spent time otherwise used on predator interference to pursue more attacks on prey organisms to increase feeding and maintain a positive energy balance. Warm-adapted predators with potentially lower energetic demands can spend more time on predator interactions resulting in lower attack coefficients at high experimental temperatures. Lower attack rates lead to reduced top-down pressure, potentially stabilising the predator-prey interaction. However, the type 3 functional response counteracts any destabilising effects of attack rate by releasing top-down pressure on low prey densities but limiting energy flow to higher trophic levels (Rall *et al.*, 2008).

Handling times are determined by digestion speed (Jeschke *et al.*, 2002) and decrease with experimental temperature due to increased speed of biochemical reactions (Thompson, 1978; Vucic-Pestic *et al.*, 2011; Lang *et al.*, 2012; Sentis *et al.*, 2015). Since body size is a strong determinant of handling time, small, warm-adapted predators have higher handling times compared to predators adapted to colder temperatures and, therefore, have bigger body sizes (Rall *et al.*, 2012). Physiological adaptation of handling times leads to steeper decrease in warm adapted predators (Sentis *et al.* 2015; Chapter 3). This directly translates into the steepest increase in maximum feeding rates for warm-adapted predators, with generally higher maximum feeding rates in bigger predators adapted to colder temperatures within our observed temperature range. Therefore, cold-adapted predators potentially have a stronger destabilising effect on predator-prey interactions under warming than

warm-adapted predators. Predators adapted to 25° C show lower maximum feeding rates, especially at lower experimental temperatures reducing top-down pressure with potentially stabilising effects on predator-prey interactions relative to cold adapted predators.

Interference increases with experimental temperature. At higher temperatures the swimming speed of predators increases which increases area and encounter rates leading to a higher number of interference events (Lang *et al.*, 2012). Predators adapted to lower temperatures have higher body sizes which further increases their swimming speed compared to smaller, warm-adapted predators. Especially at low experimental temperatures, predators adapted to warm temperatures showed higher rates of predator interference than predators adapted to cold temperatures. Due to a potential physiological adaptation of metabolism in warm adapted predators, their priority for energy gain in form of interactions with prey is lower than in cold-adapted predators and the time spent on predator interactions is higher. In cold adapted predators a lower energy budget due to higher metabolic demands potentially limits the time for predator interactions.

Predator interference increased with temperature reducing realised maximum feeding rates in Crowley Martin functional responses (Skalski and Gilliam, 2001). Generally, reduced feeding rates due to predator interference have a stabilising effect on predator-prey interactions by releasing top-down pressure (Rall *et al.*, 2008). Predators adapted to 15° C showed lower levels of predator interference than predators adapted to warmer temperatures within our observed temperature range. Comparably lower levels of interference in cold-adapted predators increases top-down pressure relative to warm-adapted predators leading to less stable predator-prey interactions. Predators adapted to 25° C show higher levels of interference, especially at lower experimental temperatures, with potentially stabilising effects on the predator-prey system (Hassell and May, 1973; Rosenzweig, 1973; DeAngelis *et al.*, 1975; Huisman and De Boer, 1997; Arditi *et al.*, 2004; Brose *et al.*, 2006; Rall *et al.*, 2008; Lang *et al.*, 2012). High levels of interference for cold-adapted predators at high experimental temperatures resulting from competition for food, reduces feeding rates. For cold adapted predators who are presumably under higher energetic stress, a further reduction of maximum feeding rates through interference could shorten the gap until the threshold where metabolic demands cannot be met by energy intake and predators face extinction due to starvation despite the availability of prey (Fussmann *et al.* 2014; Chapter 2).

Predation and predator interference are major forces inseparably shaping ecological as well as evolutionary processes (Gause, 1934; Yoshida *et al.*, 2003). Our data suggests that adaptation to higher temperatures and its effect on functional response parameters as well as predator interference potentially stabilises predator-prey interactions. Comparably high levels of predator interference and low maximum feeding rates, especially at cold experimental temperatures in warm adapted predators, suggest that adaptation to

temperature improves the overall energy budget of predators adapted to warm temperatures potentially increasing the critical threshold temperature of temperature induced extinction through energetic imbalance. However, adaptation of body size shifts predator-prey populations and entire food webs towards smaller species (Daufresne *et al.*, 2009; Yvon-Durocher *et al.*, 2011; Brose *et al.*, 2012). Further, interference limits the energy flow to higher trophic levels which could mechanistically explain food webs with smaller species, fewer links and lower trophic levels under warming (Petchey *et al.*, 1999; Petchey and Belgrano, 2010).

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Part III.

General discussion

Chapter 5.

Discussion

Climate change is progressing fast, threatening biodiversity world wide (IPCC, 2014; Parmesan, 2006). Species extinctions can be caused by a vast variety of different mechanisms, many of which are still not fully understood. Changes in temperature pose a threat on the fragile interplay of biological rates driving species interactions and population dynamics. While climate change has the potential to trigger rapid evolution (Lohbeck *et al.*, 2012; Schaum *et al.*, 2014; Geerts *et al.*, 2015), the impact of potentially changed species interactions, and their impact on population stability and species interaction dynamics is a crucial aspect. During my PhD, I designed microcosm experiments in a microbial predator-prey system to investigate the influence of temperature on predator-prey interactions and interaction strengths in time series experiments followed by adaptation studies emphasising the importance of temperature adaptation in predators to persist in a changing world.

Previously, studies suggested an increase in population oscillation in predator prey interactions with warming (Vasseur and McCann, 2005). Observed waves of predator extinction in microcosm experiments (Petchey *et al.*, 1999) were explained by high fluctuations in population abundances (Vasseur 2005, Fussmann 2000). However, these results were not corroborated by the vast majority of empirical data and contradicting studies (Rall *et al.*, 2010; Binzer *et al.*, 2012) creating a gap in mechanistic understanding of the underlying processes including the changing interplay of biological rates with temperature. Therefore, temperature dependencies for carrying capacity, metabolism and the feeding parameters half-saturation density and maximum feeding rate were drawn from a new global database containing data from different phyla across different ecosystems. Their temperature dependencies were calculated and fed into a bioenergetic model (Otto *et al.*, 2007; Boit *et al.*, 2012; Schneider *et al.*, 2012). After repeating the simulation one million times with randomly drawn parameter combinations the outcome was classified into categories of increased or decreased oscillations and predator persistence or extinction. In cases where half-saturation densities decreased faster with warming than carrying capacities, top-down pressure of the predator on its prey was increased and therefore, systems were destabilised. Opposite to previous suggestions, this occurred only in 8.9 % of

all simulations. In the vast majority of simulations, where carrying capacities decreased faster with increasing temperatures than half-saturation densities, top-down pressure is released and warming has a stabilising effect on predator-prey dynamics moving them from oscillations to equilibrium dynamics which was corroborated by my empirical time series experiments. However, despite stabilising effects on population oscillations, predators went into extinction with increasing temperatures in 73.6 % of the simulations. This is caused by an increasing mismatch of maximum feeding rates and metabolic demands with rising temperatures. Metabolism increases significantly more with warming than maximum feeding rates leading to predator extinction through starvation, especially in high trophic predators (Rall *et al.*, 2010; Binzer *et al.*, 2012; Fussmann *et al.*, 2014). Therefore, despite its stabilising effect on population dynamics in predator-prey interactions, warming can have a detrimental effect on the biodiversity of high trophic predators (Purvis *et al.*, 2000; Cardillo *et al.*, 2005). While for conservation biologists it poses a great challenges to detect seemingly stable populations close to their threshold temperature, it raises the question how organisms can potentially avoid extinction scenarios through adaptation to changing temperatures.

In order to elucidate not only the impact of increasing temperatures on feeding parameters but also possible effects of temperature adaptation I conducted functional response experiments with predators adapted to different temperatures. After 20 generations, predators adapted to higher temperatures showed the steepest increase in maximum feeding rates with rising experimental temperature compared to predators adapted to lower temperatures. My results suggest, that predators adapted to higher temperatures can develop higher activation energies of maximum feeding rates when exposed to higher temperatures. The increase in maximum feeding rates with experimental temperature exceeds the estimated increase of metabolic rates with increasing temperatures and might buffer a potential mismatch. Lower feeding rates of warm adapted predators at low experimental temperatures than for cold adapted predators could have potentially stabilising effects on predator prey interactions short-term. However, predators adapted to higher temperatures showed significantly lower body sizes after approximately 20 generations than predators adapted to lower experimental temperatures. Besides lowering the metabolic demands of an individual (Kleiber, 1932; Gillooly *et al.*, 2001; Brown *et al.*, 2004) and, with that, potentially evading extinction through starvation at high experimental temperatures, predators with smaller body sizes eventually lower energy fluxes into higher trophic levels. However, regarding population stability in predator-prey systems, attack rates and feeding rates influence half-saturation densities and the interplay of half-saturation densities relative to carrying capacity control the energy flux through trophic levels (Binzer *et al.*, 2012). In my experiments, handling times increased with experimental temperature with no significant distinction between predators adapted to different temperatures although we

expected activation energies of half-saturation densities to be on average neutral (Fussmann *et al.*, 2014). Since I used more than one predator individual per functional response treatment, this observation might be due to predator interference. Predator interference is a common pattern in natural systems (Skalski and Gilliam, 2001; Ginzburg and Jensen, 2008) and, therefore, may play a vital role in understanding predator-prey dynamics. However, it has hardly been investigated in the context of climate warming and never to date in the context of possible adaptation to warming.

To close this gap, I conducted functional response experiments along an experimental temperature gradient with predators adapted to different temperatures in different densities. To choose the best model to describe my empirical data, I compared the analyses with a classic Holling type 2 and type 3 functional response with the Beddington-DeAngelis and Crowley-Martin interference model as type 2 and type 3 functional response. Compared to type 2 functional responses, type 3 functional responses have a stabilising effect on predator-prey interactions but only at low prey densities, limiting the energy transfer to higher trophic levels (Yodzis and Innes, 1992; Williams and Martinez, 2004; Rall *et al.*, 2008). Predator interference reduces interaction strengths (Hassell and May, 1973; DeAngelis *et al.*, 1975) and has the potential to dampen population oscillations, stabilising entire food webs (Rall *et al.*, 2008) with positive effects on species richness and food web connectance (DeAngelis *et al.*, 1975; Nunney, 1980; Skalski and Gilliam, 2001; Eklöf and Ebenman, 2006). Compared to the Beddington-DeAngelis interference model, which can have stabilising effects at low prey densities, Crowley-Martin interference, the model describing my empirical data best, potentially stabilises predator-prey dynamics also at high prey densities by reducing maximum feeding rates and top-down pressure, stabilising until higher densities are reached. Further, with predator competition factored in, half-saturation densities for predators adapted to warmer temperatures increased with experimental temperature and decreased for predators adapted to colder temperatures. Regarding the energy flux controlled by the interplay of carrying capacity and half-saturation density (Binzer *et al.*, 2012), a further decrease in half-saturation density for predators adapted to cold temperatures could potentially have destabilising effects on the predator-prey interaction. For warm adapted predators, an increase in half-saturation density with experimental temperatures would therefore have a stabilising effect on population dynamics within the predator-prey interaction. Further, predators adapted to higher temperatures showed the steepest increase in maximum feeding rates with experimental temperature. However, within the measured temperature frame, they had the lowest maximum feeding rates compared to colder adapted predators. Predator interference increased fastest with experimental temperature in cold adapted predators, while warm adapted predators showed the highest levels of predator interference at low and medium experimental temperatures. Lowered levels of maximum feeding rate together with high levels of predator interference in warm adapted predators,

especially at cold and medium experimental temperatures, suggests an adaptation of metabolism to higher temperatures. With lowered metabolic demands, predators adapted to warmer temperatures are able to spend more time on predator interference on the expense of feeding interactions than their cold adapted counterparts. On behalf of potential consequences on population dynamics, reduced feeding rates and increased levels of predator interference, adaptation to higher temperature may have stabilising effects on predator-prey interactions. Whether this adaptation of energy gain to higher temperatures is solely due to reduced body sizes or also an effect of physiological adaptation needs to be explored.

Based on my results, I hypothesise that warming has stabilising effect on predator-prey interactions in a majority of cases across different taxa based on the faster increase of half-saturation density than of carrying capacity with warming, determining the energy flux across trophic levels. A potential mismatch between energy gain and energy intake, described by metabolism and maximum feeding rate, may threaten especially high trophic level predators with extinction through starvation. However, through an adaptation of maximum feeding rates as well as potentially metabolism, predators may be able to avoid such extinction scenarios when given the time to adapt to changing temperatures. The trend towards smaller body masses in predators, however, could potentially make them more vulnerable to further, more sudden increases in temperature in the future since the effect of temperature is generally more challenging for smaller organisms with greater volume to surface ratios. This would not only corroborate the trend towards food webs with smaller organisms and fewer links (Petchey *et al.*, 1999; Petchey and Belgrano, 2010) but also findings that taxa adapted to tropical environments might be more vulnerable to short-term changes in temperature (Williams *et al.*, 2007; Mayhew *et al.*, 2008). While my empirical data is based on a microbial predator-prey system, which is of great importance as a basal resource in many ecosystems on its own, the more generalised mechanistic approach supported by an extensive database provides helpful insight into the greater scope of population dynamics across different taxa and increase our ecological understanding of predator-prey interactions.

Outlook

While often documented on its own, either from a prey's (McPeek *et al.*, 1996; Yoshida *et al.*, 2003; Abrams and Walters, 2010) or a predator's perspective (Sentis *et al.*, 2015), a study combining prey adaptation with predator adaptation to climate change could deliver further insights into the mechanistic understanding of population dynamics under climate change. Temperature performance curves of predators adapted to different temperatures as well as microscopic analyses of movement speed and interaction times of *Tetrahymena pyriformis* will be helpful to verify the hypotheses drawn from Chapter 4. Further, the

microbial system presents a great opportunity to assess also possible genetic and epigenetic monitoring of the adaptation process to understand its underlying mechanisms (Nowacki *et al.*, 2007). In a changing world it is tremendously important to understand adaptation processes especially since most species do not only face one stressor but multiple stressors at a time. Adaptation to one stressor has shown to increase the probability of further adaptations to other stressors (Foo *et al.*, 2012) and can potentially sustain endangered species in a rapidly changing world.

Part IV.

Appendix

Ecological stability in response to warming

Simulations

We used a bioenergetic predator-prey model, where the biomass-densities of a prey R and its predator C follow

$$B'_R = r_R B_R(1 - \frac{B_R}{K}) - \frac{y_{CR} B_R}{B_{0_{CR}} + B_R} B_C \tag{1}$$

and

$$B'_C = \epsilon \frac{y_{CR} B_R}{B_{0_{CR}} + B_R} B_C - x_C B_C \tag{2}$$

where B'_R and B'_R are the changes in biomass density of prey and predator $[g/m^2]$, respectively. r_R is the population growth rate of R $[s^{-1}]$, K is the carrying capacity $[g/m^2]$, y_{CR} is maximum consumption rate of C on R $[s^{-1}]$, B_0 is the half-saturation density $[g/m^2]$, ϵ is the dimensionless assimilation efficiency (0.85 for carnivores) and is x_c the metabolic rate of the predator $[s^{-1}]$. In this kind of biomass model, the metabolic rate of the predator population is parameterised as biomass loss due to respiration, whereas metabolic and death rates of the resource are included in the maximum growth rate. Resource mortality is assumed to be caused only by predation as described by the functional-response term.

Following metabolic theory, we accounted for body-size and temperature dependencies of the rates:

$$r_R = r_0 e^{E_r \frac{T - T_0}{kTT_0}} \tag{3}$$

$$K_R = K_0 e^{E_K \frac{T - T_0}{kTT_0}} \tag{4}$$

$$y_{CR} = y_0 e^{E_y \frac{T - T_0}{kTT_0}} \tag{5}$$

$$B_{0_{CR}} = B_{0_0} e^{E_{B_0} \frac{T - T_0}{kTT_0}} \tag{6}$$

$$x_C = x_0 e^{E_x \frac{T - T_0}{kTT_0}} \tag{7}$$

r_0, K_0, y_0, B_{0_0} and x_0 are mass dependent normalisation constants calculated for the intercept temperature (T_0) of 293.15 K and a species with a body mass of 100 mg feeding on a 1 mg prey.

Within the extended writing of the Arrhenius equation, determining the temperature dependency of the rates, T defines the current temperature [K] and k is the Boltzmann constant [$8.617\ 10^{-5}\ eV\ K^{-1}$]. E_r, E_K, E_y, E_{B_0} and E_x are activation energies [eV] determining the exponent of the temperature dependencies (see Appendix Table 3).

Appendix Table 1 shows the empirically derived parameter values used in the model. Means and standard deviations of activation energies of K, y, B_0 and were taken from our database (Appendix Table 4), those of r were taken from Savage et al. (2004). Mass-dependent normalisation constants were calculated using various empirical studies: K from Meehan (2006), r from Savage et al. (2004), y and B_0 from (2012) and x from Ehnes et al. (2011).

Laboratory methods

Functional response

Functional responses were measured in 96 well plates containing bacterial suspensions in OS 1:10 without a carbon source to avoid bacterial growth. Bacteria were inserted after a serial scheme diluting the concentration for twelve times in a 1:2 ratio. After adding ciliates to a final concentration of 100 cells/μl, the experiment was started in a M200 plate reader (Tecan, Mä nnedorf, Switzerland). The total volume of one sample was 100 μl. Six treatments of each dilution step received ciliate solution yielding a final concentration of 100 predators/μl. Two treatments of each dilution step were used as control treatments without predators receiving the same amount of OS 1:10. Functional response experiments were replicated at 15° C, 20° C, 25° C and 30° C. Optical density (OD600) and green fluorescence (excitation, 485 nm; emission, 520 nm; gain, 80) were recorded every five minutes over a time span of 8 hours. With the help of a calibration series where OD-values and green fluorescence signals were compared to cell counts these measurements were

converted to cell concentrations. Time span utilised for statistical analysis was two hours after start, ending eight hours later, to exclude transient dynamics in the beginning of the experiment. Plates were shaken every two minutes ensure homogeneous suspensions.

Statistics

Functional response analyses

Statistical analyses of the microcosm functional response experiments were conducted with ***R*** (R Core Team, 2014). We used the Roger's random equation to analyse the functional response data, due to decreasing cell counts during the time of the experiment (Royama, 1971; Pinhero and al, 2011):

$$N_e = N_0(1 - e^{aN(hN_e - P\tau)}) \tag{8}$$

In this equation, N_e represents consumed prey, N_0 initial prey density, P the predator density. h handling time, a attack rate, while τ is the over all time of the experiment. This recursive equation was solved by using the additional packages NLME (non-linear mixed effects, Bolker 2012) and EMDBOOK (Bolker, 2007).

$$N_e = N_0 - W\frac{(ahN_0e^{-a(P\tau - hN_0)})}{ah} \tag{9}$$

In this equation W stands for the Lambert W function (Bolker, 2007). Attack rates a and handling times h follow a deduced form of the Arrhenius equation (Vasseur and McCann, 2005):

$$h = h_0e^{E_h\frac{(T - T_0)}{kTT_0}} \tag{10}$$

$$a = a_0e^{E_a\frac{(T - T_0)}{kTT_0}} \tag{11}$$

where h_0 and a_0 are normalisation constants at the intercept temperature, T_0 (293.15 K). T is the temperature (in K), k is the Boltzmann constant ($8.62 * 10^{-5}eV^{-1}$) and E_h and E_a are activation energies in eV.

Supplementary results

Simulations

In the main document, we used overall mean values of activation energies for the physiological rates to give an first impression of their dynamical consequences (Chapter 2, Figure 2.2). As there are four different possible dynamical outcomes depending on the combination of activation energies (increasing or decreasing oscillations with warming, both either with persisting or extinct predators, see Chapter 2, Figure 2.3), we replicated the simulations with the mean values corresponding to each of the cases (Figures 1 - 4).
Please note that the time series shown in this supplement focus on the long-term dynamics, whereas those in the main text were reduced to initial dynamics to allow comparisons with experimental data. In the Appendix Figures 1 - 4, the system-state at the end of the time series is therefore directly related to the one shown in the corresponding bifurcation diagram.
Appendix Figures 1 and 2 show the warming response as it was predicted by former studies (Vasseur and McCann, 2005). In these scenarios, foraging efficiency reacts more strongly to warming than the maximum prey density (compare Figure 2.3, Chapter 2). Therefore, warming increases top-down pressure and the system is destabilised (i.e., the amplitudes of the oscillations decrease). The occurring oscillations are comparable to others that originate from increased system-energy flow relative to the consumer loss term as described under the principle of energy flux or the paradox of enrichment (Rip and McCann, 2011; Rosenzweig, 1971).
Appendix Figure 3 shows that there are scenarios with an equilibrium state over the whole temperature range, whereas Appendix Figure 4 shows the most frequent case of warming stabilising population dynamics at the risk of predator extinction at high temperatures.

Functional response measurements

Per capita feeding rates increased slightly with warming (Appendix Figure 6). More precisely, attack rates showed no significant increase, whereas handling times decreased significantly with a rather shallow slope (Appendix Table 2).

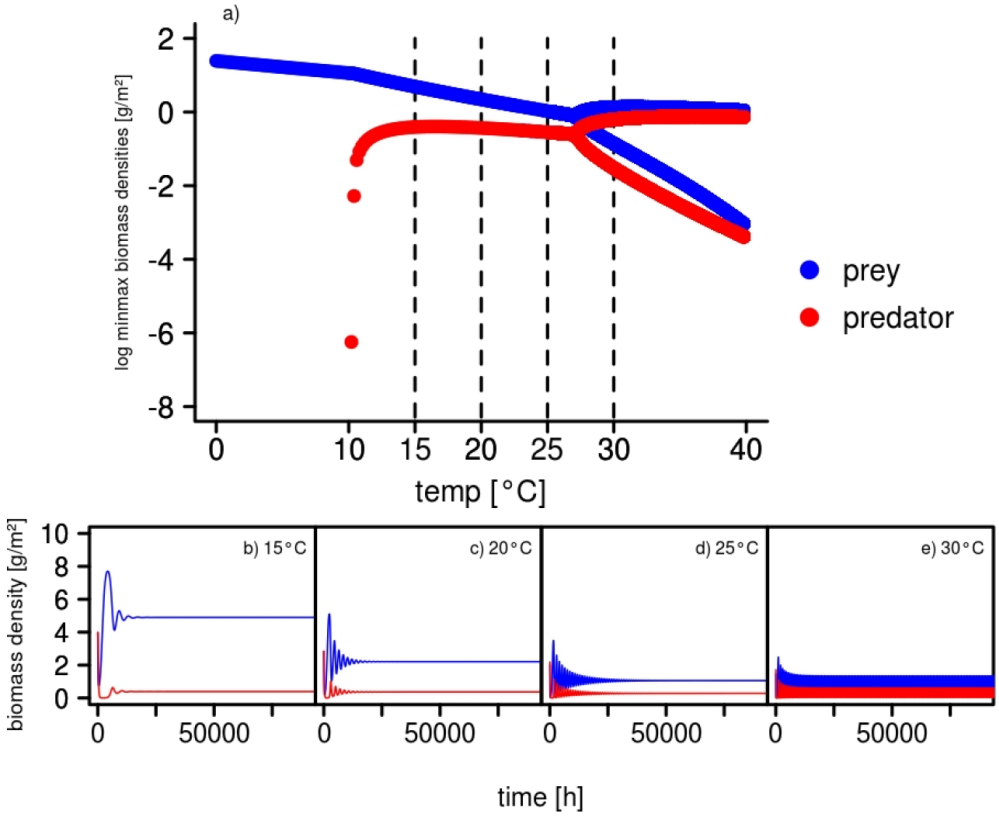

Figure 1 – Destabilising without extinction. E_k = -0.508, E_r = 0.840, E_x = 0.428, E_{mi} = 0.708, E_{B_0} = -0.678. **a** Bifurcation diagram showing the minimum and maximum values of logarithmic biomass densities within a time-series in dependence of temperature. Dashed lines indicate the temperatures of which **b-e** show the corresponding time-series. Blue: prey densities; red: predator densities.

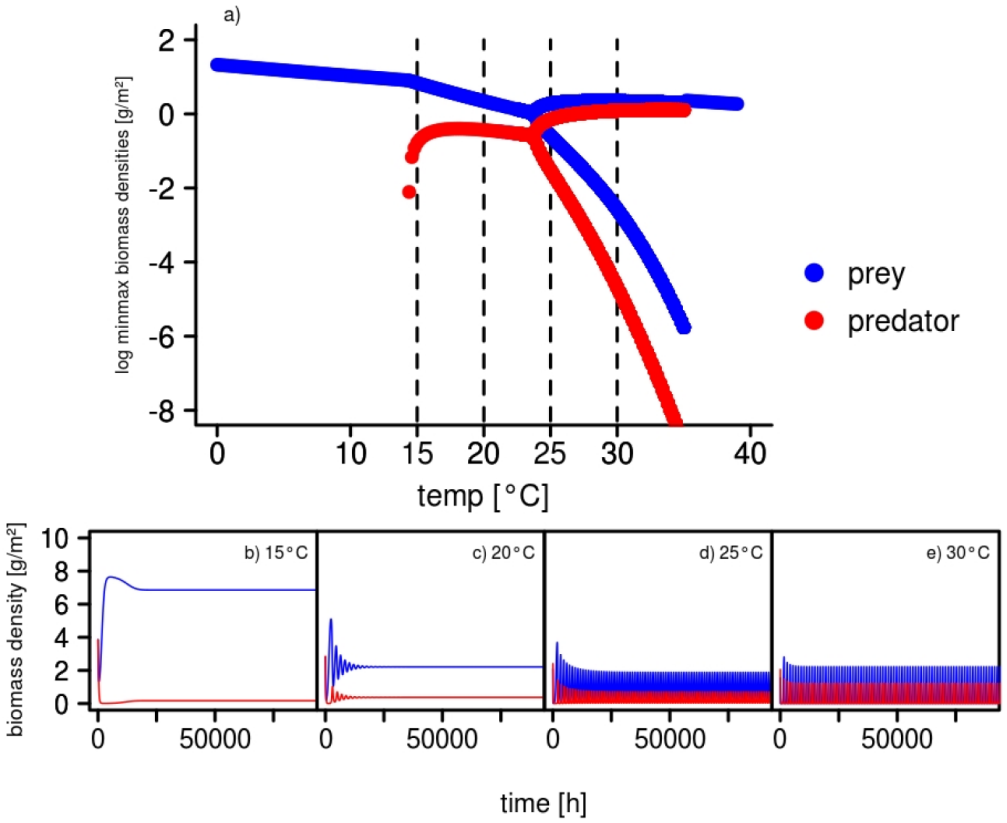

Figure 2 – Destabilising with extinction. E_k = -0.459, E_r = 0.840, E_x = 0.512, E_{mi} = 0.973, E_{B_0} = -0.817. **a** Bifurcation diagram showing the minimum and maximum values of logarithmic biomass densities within a time-series in dependence of temperature. Dashed lines indicate the temperatures of which **b-e** show the corresponding time-series. Blue: prey densities; red: predator densities.

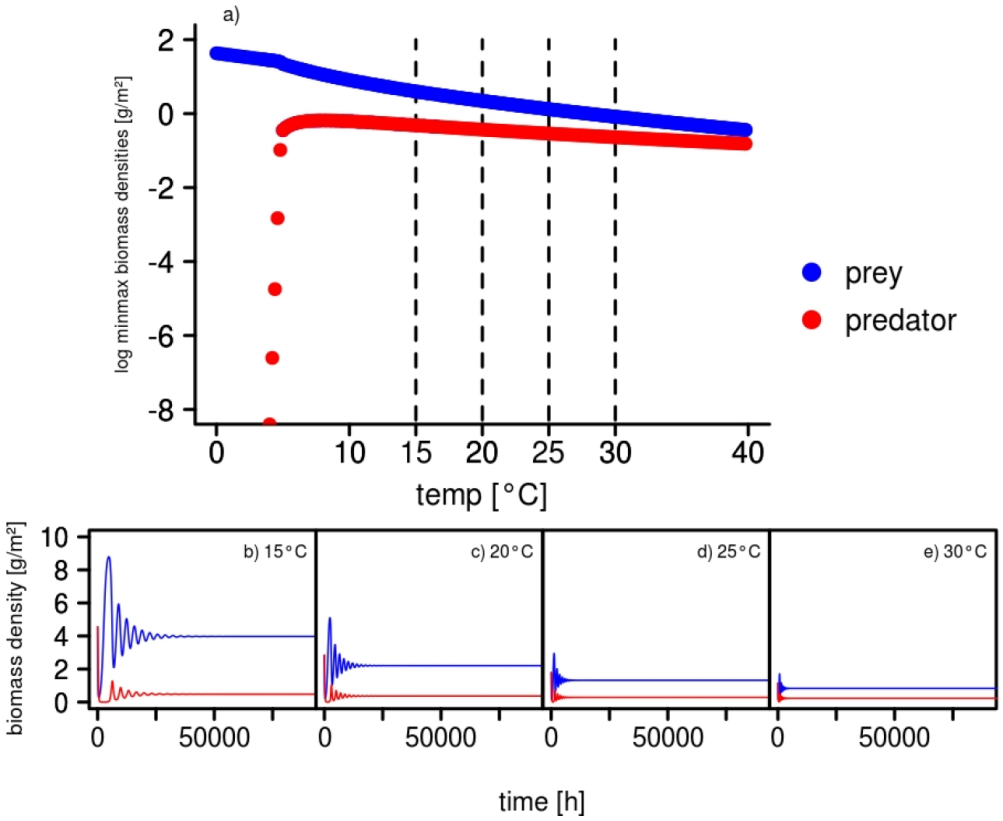

Figure 3 – Stabilising without extinction. E_k = -0.707, E_r = 0.840, E_x = 0.482, E_{mi} = 0.818, E_{B_0} = -0.270. **a** Bifurcation diagram showing the minimum and maximum values of logarithmic biomass densities within a time-series in dependence of temperature. Dashed lines indicate the temperatures of which **b-e** show the corresponding time-series. Blue: prey densities; red: predator densities.

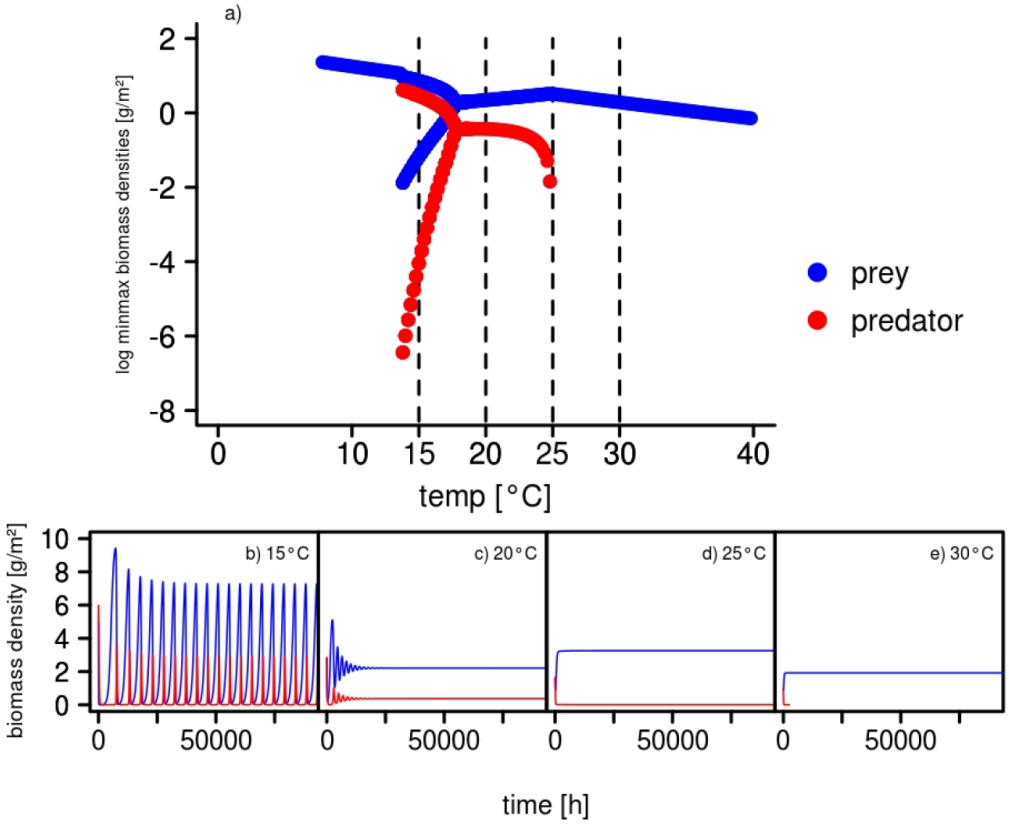

Figure 4 – Stabilising with extinction. E_k = -0.823, E_r = 0.840, E_x = 0.696, E_{mi} = 0.338, E_{B_0} = 0.001. **a** Bifurcation diagram showing the minimum and maximum values of logarithmic biomass densities within a time-series in dependence of temperature. Dashed lines indicate the temperatures of which **b-e** show the corresponding time-series. Blue: prey densities; red: predator densities.

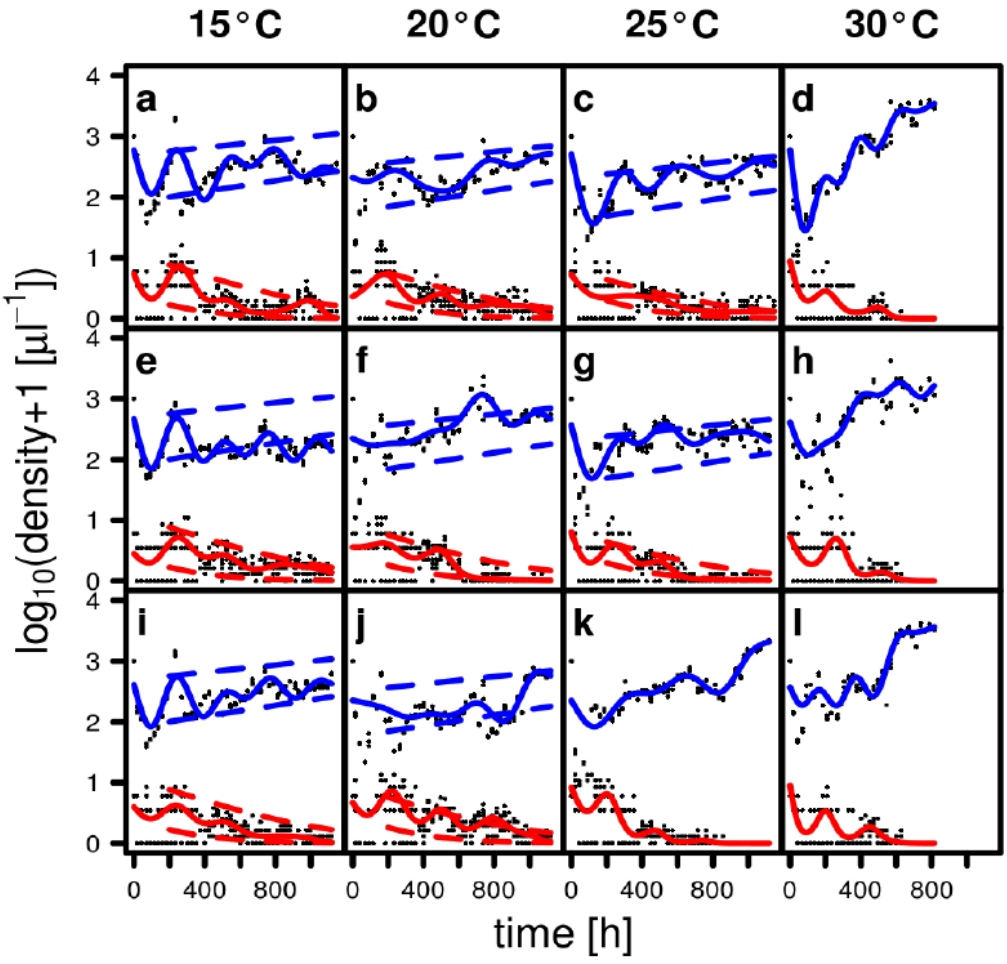

Figure 5 – Time Series of *Tetrahymena pyriformis* and *Pseudomonas fluorescens* CHA19-gfp Replicates of the time series at **a**, **e**, **i** 15° C, **b**, **f**, **j** 20° C, **c**, **g**, **k** 25° C and **d**, **h**, **l** 30° C fitted with a gam-model with Poisson distribution. Red lines show abundances of the predator T. pyriformis over time while blue lines show prey densities. Dotted lines in the according colours show quantile regressions.

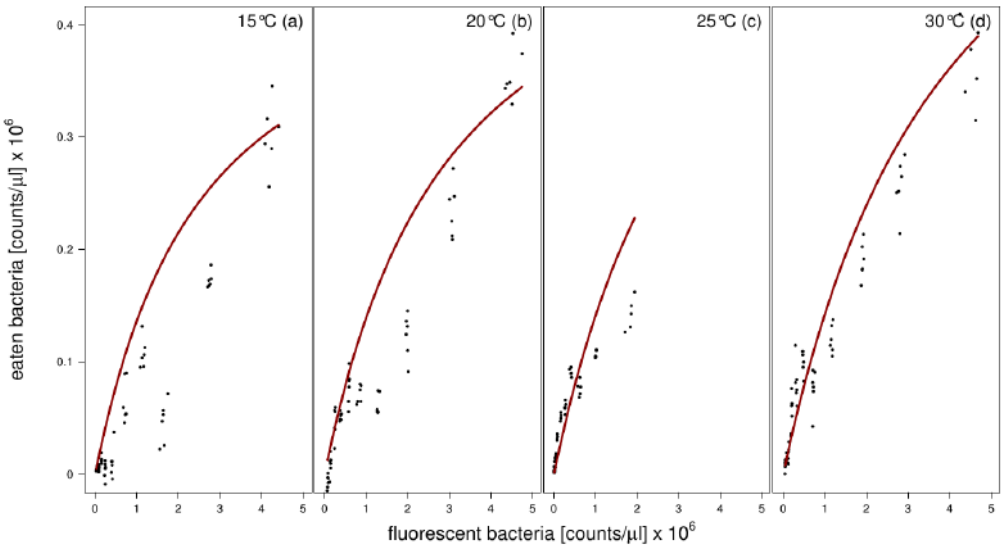

Figure 6 – **Functional response results for after 60 minutes.** Graphs show the feeding rates in dependence of bacterial density (x-axis) at, **a**, 15° C, **b**, 20° C, **c**, 25° C and **d**, 30° C.

Supplementary tables

Table 1 – Model parameters

	normalisation constant	E[mean]	SD_{E_a}
K	5.623	-0.772	0.357
r_R	-8.715 10^{-7}	0.84	0.4
y_{CR}	-8.408 10^{-6}	0.467	0.443
$B_{0_{CR}}$	3.664	-0.114	0.639
x_C	2.689 10^{-6}	0.639	0.286

Table 2 – Activation Energies as estimated by functional response fitting.

parameters	estimate	s.e.	p
a_0	6 10^{-7}	6 10^{-2}	< 0.001
E_a	-0.03	0.036	0.38
h_0	0.61	0.026	< 0.001
E_h	-0.19	0.051	< 0.001

Table 3 – Statistical estimates for the analyses of the temperature dependence of amplitude strength. Effects are given for the ln-transformed normalised amplitude values, the Arrhenius temperature (activation energy: E_{linear}), the squared Arrhenius temperature (activation energy: $E_{squared}$), the amplitude sequence number (slope: $a_{sequence}$), as well as the allowed interactions.

	estimate	Std.Error	DF	t-value	p-value
intercept	-1.07	0.54	64	-1.98	0.0517
E_{linear}	3.99	1.42	5	2.82	< 0.05
$E_{squared}$	5.39	1.68	5	3.20	< 0.05
$a_{sequence}$	0.03	0.17	64	0.19	0.8477
$E_{linear} : a_{sequence}$	-1.21	0.42	64	-2.92	< 0.01
$E_{squared} : a_{sequence}$	-1.39	0.51	64	-2.75	< 0.01

Table 4 – Statistical outputs of regression analysis

rate type	taxonomic group	predator species	resource species	E	s.e.(E)	P-value (E)	n	temp levels	temp range	R^2	reference
maximum resource density	Arthropoda	*NA*	*Aedes albopictus*	-1.38	0.36	0.009	8	3	4	0.71	Alto and Juliano 2001
maximum resource density	Bacteria	*NA*	*Aerobacter aerogenes*	-0.71	0.18	0.012	7	7	35	0.75	Greene and Jezeski 1953
maximum resource density	Bacteria	*NA*	*Enterococcus faecium*	-0.9	0.34	0.029	10	10	44	0.47	Zanoni *et al.* 1993
maximum resource density	Bacteria	*NA*	*Lactobacillus plantarum*	-0.67	0.15	0.001	16	9	18.5	0.59	Zwietering *et al.* 1991
maximum resource density	Bacteria	*NA*	*Pseudomomas1*	-0.68	0.51	0.253	6	6	30	0.31	Greene and Jezeski 1953
maximum resource density	Bacteria	*NA*	*Pseudomonas2*	-0.29	0.25	0.304	6	6	30	0.26	Greene and Jezeski 1953
foraging efficiency	Arthropoda	*Acartia hudsonica*	*Thalassiosira constricta*	0.52	0.2	0.12	4	4	12	0.77	Durbin and Durbin 1992; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Amblyseius californicus*	*Tetranychus urticae*	0.39	0.16	0.253	3	3	10	0.85	Otoh *et al.* 2004; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Amblyseius longispinosus*	*Aponychus corpuzae*	0.07	0.09	0.477	5	5	20	0.18	Zhang *et al.* 1998; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Amblyseius longispinosus*	*Schizotetranychus nanjingensis*	0.01	0.24	0.977	6	6	25	0	Zhang *et al.* 1999; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Anisopteromalus calandrae*	*Rhyzopertha dominica*	-0.47	0.47	0.424	4	4	15	0.33	Menon *et al.* 2002; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Anisopteromalus calandrae*	*Sitophilus zeamais*	0.23	0.07	0.174	3	3	10	0.93	Smith 1994; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Aphidius colemani*	*Aphis gossypii*	0.04	0.13	0.788	5	5	20	0.03	Zamani *et al.* 2006; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Aphidius matricariae*	*Aphis gossypii*	0.05	0.16	0.753	5	5	20	0.04	Zamani *et al.* 2006; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Calathus fuscipes*	*Alphitobius diaperinus*	0.45	0.36	0.286	6	6	25	0.27	Vucic-Pestic *et al.* 2011; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Calathus fuscipes*	*Drosophila hydei*	0.02	0.06	0.799	6	6	25	0.02	Vucic-Pestic *et al.* 2011; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Celithemis fasciata*	*Chironomus tentans*	0	0.05	0.982	3	3	10	0	Gresens *et al.* 1982; Rall *et al.* 2012

rate type	taxonomic group	predator species	resource species	E	s.e.(E)	P-value (E)	n	temp levels	temp range	R^2	reference
foraging efficiency	Arthropoda	*Cephalonomia waterstoni*	*Cryptolestes ferrugineus*	-0.19	0.08	0.253	3	3	10	0.85	Flinn 1991; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Chaoborus americanus*	*Daphnia pulex*	-0.33	0.41	0.569	3	3	10	0.39	Spitze 1985; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Chaoborus americanus*	*Daphnia pulex*	-0.3	0.46	0.629	3	3	10	0.3	Spitze 1985; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	-0.12	0.17	0.557	5	5	20	0.13	Xia *et al.* 2003; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	-0.2	0.16	0.295	5	5	20	0.35	Xia *et al.* 2003; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	-0.3	0.07	0.02	5	5	20	0.87	Xia *et al.* 2003; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	-0.27	0.1	0.073	5	5	20	0.71	Xia *et al.* 2003; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	-0.4	0.21	0.156	5	5	20	0.54	Xia *et al.* 2003; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	-0.66	0.13	0.016	5	5	20	0.89	Xia *et al.* 2003; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	-0.38	0.04	0.002	5	5	20	0.97	Xia *et al.* 2003; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	-0.3	0.05	0.009	5	5	20	0.93	Xia *et al.* 2003; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	-0.59	0.06	0.002	5	5	20	0.97	Xia *et al.* 2003; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	-0.35	0.05	0.005	5	5	20	0.95	Xia *et al.* 2003; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	-0.54	0.09	0.008	5	5	20	0.93	Xia *et al.* 2003; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	-0.7	0.08	0.003	5	5	20	0.96	Xia *et al.* 2003; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	-0.55	0.1	0.01	5	5	20	0.92	Xia *et al.* 2003; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	-0.54	0.08	0.006	5	5	20	0.94	Xia *et al.* 2003; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	-0.68	0.08	0.004	5	5	20	0.96	Xia *et al.* 2003; Rall *et al.* 2012

rate type	taxonomic group	predator species	resource species	E	s.e.(E)	P-value (E)	n	temp levels	temp range	R^2	reference
foraging efficiency	Arthropoda	*Coenosia attenuata*	*Drosophila melanogaster*	-0.52	0.21	0.246	3	3	12	0.86	Gilioli *et al.* 2005; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Coleomegilla maculata*	*Leptinotarsa decemlineata*	-1.97	0.71	0.22	3	3	6	0.89	Munyaneza and Obrycki 1997; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Coleomegilla maculata*	*Myzus persicae*	-1.22	0.24	0.007	6	6	18.9	0.86	Sentis *et al.* 2012; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Cycloneda sanguinea*	*Aphis gossypii*	0.19	0.85	0.858	3	3	10	0.05	Işikber 2005; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Encarsia formosa*	*Bemisia tabaci*	0.5	0.31	0.352	3	3	12	0.72	Enkeegard 1994; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Harpalus rufipes*	*Alphitobius diaperinus*	0.43	0.29	0.216	6	6	25	0.35	Vucic-Pestic *et al.* 2011
foraging efficiency	Arthropoda	*Harpalus rufipes*	*Drosophila hydei*	-0.21	0.31	0.533	6	6	25	0.1	Vucic-Pestic *et al.* 2011; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Ischnura elegans*	*Daphnia magna*	0.2	0.18	0.327	6	6	22.5	0.24	Thompson 1978; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Neoseiulus californicus*	*Tetranychus urticae*	0.36	0.09	0.061	4	4	15	0.88	Ahn *et al.* 2010; Rall *et al.* 2012
foraging efficiency	Fish	*Perca fluviatilis*	*Chaoborus obscuripes*	-0.38	0.18	0.171	4	4	9	0.69	Persson 1986; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Piona exigua*	*Ceriodaphnia dubia*	0	0	0.377	4	4	12	0.39	Butler and Burns 1993; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Piona exigua*	*Ceriodaphnia dubia*	0	0	0.119	4	4	12	0.78	Butler and Burns 1993; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Piona exigua*	*Daphnia carinata*	0	0.02	0.9	3	3	7	0.02	Butler and Burns 1993; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Podisus maculiventris*	*Spodoptera exigua*	-0.06	0.09	0.627	3	3	9	0.31	Mohaghegh *et al.* 2001; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Podisus nigrispinus*	*Spodoptera exigua*	0.43	0.77	0.676	3	3	9	0.24	Mohaghegh *et al.* 2001; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Pterostichus melanarius*	*Alphitobius diaperinus*	0.69	0.35	0.121	6	6	25	0.49	Vucic-Pestic *et al.* 2011; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Pterostichus melanarius*	*Drosophila hydei*	-0.18	0.12	0.212	6	6	25	0.36	Vucic-Pestic *et al.* 2011; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Ranatra dispar*	*Anisops deanei*	-0.63	0.13	0.134	3	3	10	0.96	Bailey 1989; Rall *et al.* 2012

rate type	taxonomic group	predator species	resource species	E	s.e.(E)	P-value (E)	n	temp levels	temp range	R^2	reference
foraging efficiency	Fish	*Rutilus rutilus*	*Chaoborus obscuripes*	-0.62	0.52	0.356	4	4	9	0.42	Persson 1986; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Scolothrips takahashii*	*Tetranychus urticae*	0.22	0.17	0.417	3	3	10	0.63	Otoh *et al.* 2004; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Scolothrips takahashii*	*Tetranychus viennensis*	1.06	0.01	0.003	3	3	10	1	Ding-Xu *et al.* 2007; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Scolothrips takahashii*	*Tetranychus viennensis*	-0.09	0.05	0.215	4	4	15	0.62	Ding-Xu *et al.* 2007; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Scymnus levaillanti*	*Aphis gossypii*	0.85	0.62	0.402	3	3	10	0.65	Işikber 2005; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Stethorus japonicus*	*Tetranychus urticae*	0.98	0.18	0.114	3	3	12	0.97	Otoh *et al.* 2004; Rall *et al.* 2012
foraging efficiency	Arthropoda	*Telenomus reynoldsi*	*Geocoris punctipes*	-0.86	0.31	0.067	5	5	15	0.73	Cave and Gaylor ????; Rall *et al.* 2012
foraging efficiency	unicells	*Tetrahymena pyriformis*	*Pseudomonas fluorescens*	0.16				4	15	2	this study
foraging efficiency	Arthropoda	*Theocolax elegans*	*Rhyzopertha dominica*	0.35	0.84	0.717	4	4	12.5	0.08	Flinn and Hagstrum 2002; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Acartia hudsonica*	*Thalassiosira constricta*	0.52	0.2	0.12	4	4	12	0.77	Durbin and Durbin 1992; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Amblyseius californicus*	*Tetranychus urticae*	0.41	0.07	0.112	3	3	10	0.97	Otoh *et al.* 2004; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Amblyseius longispinosus*	*Aponychus corpuzae*	0.23	0.08	0.062	5	5	20	0.74	Zhang *et al.* 1998; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Amblyseius longispinosus*	*Schizotetranychus nanjingensis*	0.44	0.14	0.032	6	6	25	0.72	Zhang *et al.* 1999; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Anisopteromalus calandrae*	*Rhyzopertha dominica*	1.14	0.43	0.115	4	4	15	0.78	Menon *et al.* 2002; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Anisopteromalus calandrae*	*Sitophilus zeamais*	1	0.33	0.094	4	4	15	0.82	Smith 1994; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Aphidius colemani*	*Aphis gossypii*	0.32	0.1	0.055	5	5	20	0.76	Zamani *et al.* 2006; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Aphidius matricariae*	*Aphis gossypii*	0.15	0.13	0.324	5	5	20	0.32	Zamani *et al.* 2006; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Calathus fuscipes*	*Alphitobius diaperinus*	0.27	0.04	0.02	4	4	15	0.96	Vucic-Pestic *et al.* 2011; Rall *et al.* 2012

rate type	taxonomic group	predator species	resource species	E	s.e.(E)	P-value (E)	n	temp levels	temp range	R^2	reference
maximum feeding rate	Arthropoda	*Calathus fuscipes*	*Drosophila hydei*	0.2	0.12	0.16	6	6	25	0.43	Vucic-Pestic *et al.* 2011; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Celithemis fasciata*	*Chironomus tentans*	0.29	0.04	0.023	4	4	15	0.96	Gresens *et al.* 1982; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Cephalonomia waterstoni*	*Cryptolestes ferrugineus*	-0.19	0.08	0.253	3	3	10	0.85	Flinn 1991; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Chaoborus americanus*	*Daphnia pulex*	0.57	0.32	0.327	3	3	10	0.76	Spitze 1985; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Chaoborus americanus*	*Daphnia pulex*	0.2	0.56	0.783	3	3	10	0.11	Spitze 1985; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	0.39	0.16	0.092	5	5	20	0.67	Xia *et al.* 2003; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	0.37	0.13	0.067	5	5	20	0.72	Xia *et al.* 2003; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	0.23	0.06	0.035	5	5	20	0.82	Xia *et al.* 2003; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	0.25	0.13	0.137	5	5	20	0.58	Xia *et al.* 2003; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	0.21	0.14	0.235	5	5	20	0.42	Xia *et al.* 2003; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	0.15	0.08	0.141	5	5	20	0.57	Xia *et al.* 2003; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	0.1	0.06	0.21	5	5	20	0.46	Xia *et al.* 2003; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	0.19	0.07	0.074	5	5	20	0.71	Xia *et al.* 2003; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	0.31	0.09	0.171	3	3	10	0.93	Xia *et al.* 2003; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	-0.09	0.03	0.067	4	4	15	0.87	Xia *et al.* 2003; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	-0.04	0.05	0.499	5	5	20	0.16	Xia *et al.* 2003; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	0.13	0.06	0.291	3	3	10	0.81	Xia *et al.* 2003; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	-0.04	0.03	0.257	5	5	20	0.39	Xia *et al.* 2003; Rall *et al.* 2012

rate type	taxonomic group	predator species	resource species	E	s.e.(E)	P-value (E)	n	temp levels	temp range	R^2	reference
maximum feeding rate	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	-0.07	0.01	0.029	4	4	15	0.94	Xia *et al.* 2003; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Coccinella septempunctata*	*Aphis gossypii*	0.05	0.02	0.062	5	5	20	0.74	Xia *et al.* 2003; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Coenosia attenuata*	*Drosophila melanogaster*	0.82	0.3	0.109	4	4	18	0.79	Gilioli *et al.* 2005; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Coleomegilla maculata*	*Leptinotarsa decemlineata*	0.41	0.48	0.484	4	4	8	0.27	Munyaneza and Obrycki 1997; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Coleomegilla maculata*	*Myzus persicae*	0.68	0.1	0.003	6	6	18.9	0.92	Sentis *et al.* 2012; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Cycloneda sanguinea*	*Aphis gossypii*	0.91	0.33	0.221	3	3	10	0.88	Işikber 2005; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Encarsia formosa*	*Bemisia tabaci*	1.43	0.35	0.152	3	3	12	0.94	Enkeegard 1994; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Harpalus rufipes*	*Alphitobius diaperinus*	0.33	0.06	0.007	6	6	25	0.87	Vucic-Pestic *et al.* 2011
maximum feeding rate	Arthropoda	*Harpalus rufipes*	*Drosophila hydei*	0.38	0.14	0.057	6	6	25	0.64	Vucic-Pestic *et al.* 2011; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Ischnura elegans*	*Daphnia magna*	0.71	0.22	0.032	6	6	22.5	0.72	Thompson 1978; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Neoseiulus californicus*	*Tetranychus urticae*	0.38	0.04	0.012	4	4	15	0.98	Ahn *et al.* 2010; Rall *et al.* 2012
maximum feeding rate	Fish	*Perca fluviatilis*	*Chaoborus obscuripes*	0.36	0.14	0.12	4	4	9	0.77	Persson 1986; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Piona exigua*	*Ceriodaphnia dubia*	0.63	0.17	0.063	4	4	12	0.88	Butler and Burns 1993; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Piona exigua*	*Ceriodaphnia dubia*	0.53	0.07	0.016	4	4	12	0.97	Butler and Burns 1993; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Piona exigua*	*Daphnia carinata*	1.21	0.4	0.095	4	4	12	0.82	Butler and Burns 1993; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Podisus maculiventris*	*Spodoptera exigua*	0.24	0.01	0.017	3	3	9	1	Mohaghegh *et al.* 2001; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Podisus nigrispinus*	*Spodoptera exigua*	0.75	0.44	0.338	3	3	9	0.74	Mohaghegh *et al.* 2001; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Pterostichus melanarius*	*Alphitobius diaperinus*	0.3	0.08	0.017	6	6	25	0.8	Vucic-Pestic *et al.* 2011; Rall *et al.* 2012

rate type	taxonomic group	predator species	resource species	E	s.e.(E)	P-value (E)	n	temp levels	temp range	R^2	reference
maximum feeding rate	Arthropoda	*Pterostichus melanarius*	*Drosophila hydei*	0.14	0.04	0.028	6	6	25	0.74	Vucic-Pestic *et al.* 2011; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Ranatra dispar*	*Anisops deanei*	0.56	0.33	0.23	4	4	15	0.59	Bailey 1989; Rall *et al.* 2012
maximum feeding rate	Fish	*Rutilus rutilus*	*Chaoborus obscuripes*	0.7	0.21	0.08	4	4	9	0.85	Persson 1986; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Scolothrips takahashii*	*Tetranychus urticae*	0.65	0	0.002	3	3	10	1	Otoh *et al.* 2004; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Scolothrips takahashii*	*Tetranychus viennensis*	0.52	0.08	0.025	4	4	15	0.95	Ding-Xu *et al.* 2007; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Scolothrips takahashii*	*Tetranychus viennensis*	0.46	0.09	0.041	4	4	15	0.92	Ding-Xu *et al.* 2007; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Scymnus levaillanti*	*Aphis gossypii*	1.84	0.25	0.084	3	3	10	0.98	Işikber 2005; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Stethorus japonicus*	*Tetranychus urticae*	0.94	0.17	0.117	3	3	12	0.97	Otoh *et al.* 2004; Rall *et al.* 2012
maximum feeding rate	Arthropoda	*Telenomus reynoldsi*	*Geocoris punctipes*	0.26	0.03	0.003	5	5	15	0.97	Cave and Gaylor ????; Rall *et al.* 2012
maximum feeding rate	unicells	*Tetrahymena pyriformis*	*Pseudomonas fluorescens*	0.19				4	15	2	this study
maximum feeding rate	Arthropoda	*Theocolax elegans*	*Rhyzopertha dominica*	2.11	0.45	0.042	4	4	12.5	0.92	Flinn and Hagstrum 2002; Rall *et al.* 2012
metabolism	Arthropoda	*Abax paralellepipedus*	*NA*	0.63	0.06	0	49	5	20	0.74	Ehnes *et al.* 2011
metabolism	Reptiles	*Acabthodactylus boskianus*	*NA*	0.59	0.21	0.05	7	7	30	0.79	Andrews and Pough 1985; Al-Sadoon and Spellerberg 1985*b*; White *et al.* 2006
metabolism	Reptiles	*Acanthodactylus erythrurus*	*NA*	0.51	NA	NA	4	4	15	1	Andrews and Pough 1985; White *et al.* 2006
metabolism	Reptiles	*Acanthodactylus opheodurus*	*NA*	0.65	NA	NA	3	3	15	0.98	Andrews and Pough 1985; Al-Sadoon 1986
metabolism	Reptiles	*Acanthodactylus pardalis*	*NA*	0.35	NA	NA	4	4	15	0.9	Andrews and Pough 1985; White *et al.* 2006
metabolism	Reptiles	*Acanthodactylus schmidti*	*NA*	0.6	NA	NA	3	3	15	1	Andrews and Pough 1985; Al-Sadoon 1986

rate type	taxonomic group	predator species	resource species	E	s.e.(E)	P-value (E)	n	temp levels	temp range	R^2	reference
metabolism	Reptiles	*Acanthodactylus schreiberi*	*NA*	0.34	NA	NA	4	4	15	0.97	Andrews and Pough 1985; White *et al.* 2006
metabolism	Reptiles	*Acanthodactylus scutellatus*	*NA*	0.61	NA	NA	4	4	15	0.95	Andrews and Pough 1985; White *et al.* 2006
metabolism	Reptiles	*Acanthophis praelongus*	*NA*	0.5	NA	NA	4	4	9	0.81	Andrews and Pough 1985; Bedford and Christian 1998
metabolism	Arthropoda	*Achipteria coleoptrata*	*NA*	0.85	NA	NA	4	4	15	0.94	Ehnes *et al.* 2011; Meehan 2006; Al-Sadoon and Spellerberg 1985*b*
metabolism	Arthropoda	*Achipteria holomonensis*	*NA*	1.02	NA	NA	3	3	10	0.99	Ehnes *et al.* 2011; Meehan 2006; Stamou 1986
metabolism	Arthropoda	*Achipteria oudemansi*	*NA*	0.48	NA	NA	6	6	22	0.85	Ehnes *et al.* 2011; Meehan 2006; Stamou *et al.* 1995
metabolism	Reptiles	*Acrantophis dumerili*	*NA*	0.74	NA	NA	3	3	14	1	Al-Sadoon 1986; Chappell and Ellis 1987*a*
metabolism	Amphibians	*Acris crepitans*	*NA*	0.76	0.12	0	10	3	20	0.87	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Arthropoda	*Adoristes ovatus*	*NA*	0.78	NA	NA	4	4	15	1	Ehnes *et al.* 2011; Meehan 2006; Luxton 1975
metabolism	Arthropoda	*Alaskozetes antarcticus*	*NA*	0.7	0.08	0	27	3	10	0.94	Ehnes *et al.* 2011; Block 1977; Caruso *et al.* 2010; Young 1979
metabolism	Reptiles	*Aligator mississippiensis*	*NA*	0.79	NA	NA	6	6	25	0.99	Lewis and Gatten Jr. 1985; White *et al.* 2006
metabolism	Annelida	*Allolobophora caliginosa*	*NA*	0.49	0.1	0.129	4	4	13	0.99	Byzova 1965; Phillipson and Bolton 1976; Meehan 2006; Ehnes *et al.* 2011
metabolism	Arthropoda	*Alopecosa juv.*	*NA*	0.34	0.34	0.348	12	3	7	0.13	Ehnes *et al.* 2011
metabolism	Arthropoda	*Alopecosa spec*	*NA*	0.84	0.11	0	39	5	14	0.64	Ehnes *et al.* 2011

rate type	taxonomic group	predator species	resource species	E	s.e.(E)	P-value (E)	n	temp levels	temp range	R^2	reference
metabolism	Reptiles	*Amblyrhynchus cristatus*	*NA*	0.93	0.03	0.02	4	4	15	1	Bartholomew and Lasiewski 1965; Bennett *et al.* 1975; White *et al.* 2006
metabolism	Amphibians	*Ambystoma maculatum*	*NA*	0.5	0.11	0.002	12	6	25	0.85	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Ambystoma tigrinum*	*NA*	0.49	0.18	0.017	14	6	20	0.55	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Fish	*Ameiurus nebulosus*	*NA*	0.62	0.02	0	6	3	20	1	Bokma 2004; White *et al.* 2006
metabolism	Reptiles	*Amphibolurus barbatus*	*NA*	0.54	NA	NA	3	3	17	0.99	Bartholomew and Tucker 1963; Andrews and Pough 1985; White *et al.* 2006
metabolism	Amphibians	*Amphiuma means*	*NA*	0.8	0.11	0	14	9	25	0.86	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Aneides hardii*	*NA*	0.37	NA	NA	5	5	20	0.92	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Fish	*Anguilla japonica*	*NA*	0.83	NA	NA	29	16	17	0.92	Bokma 2004; White *et al.* 2006
metabolism	Reptiles	*Anguis fragilis*	*NA*	0.37	NA	NA	3	3	15	1	Al-Sadoon and Spellerberg 1985*a*; Andrews and Pough 1985; White *et al.* 2006
metabolism	Reptiles	*Anniella pulchra*	*NA*	0.41	0.08	0.035	5	5	24	0.95	Kamel and E. 1983; Fusari 1984; Andrews and Pough 1985; White *et al.* 2006
metabolism	Reptiles	*Antaresia childreni*	*NA*	0.9	0.05	0.038	4	4	9	1	Bedford and Christian 1998; White *et al.* 2006
metabolism	Reptiles	*Antaresia stimsoni*	*NA*	0.19	0.2	0.521	4	4	9	0.78	Bedford and Christian 1998; White *et al.* 2006
metabolism	Annelida	*Aporectodea caliginosa*	*NA*	0.54	0.05	0	53	8	25	0.74	Ehnes *et al.* 2011
metabolism	Annelida	*Aporectodea rosea*	*NA*	0.64	0.19	0.007	14	3	10	0.68	Ehnes *et al.* 2011
metabolism	Arthropoda	*Armadillidium vulgare*	*NA*	0.69	0.08	0	49	12	25	0.68	Edney 1964; Reichle 1968; Saito 1969; Al-Dabbagh 1976; Meehan 2006; Ehnes *et al.* 2011

rate type	taxonomic group	predator species	resource species	E	s.e.(E)	P-value (E)	n	temp levels	temp range	R^2	reference
metabolism	Reptiles	*Aspidites melanocephalus*	*NA*	0.87	NA	NA	4	4	9	1	Bedford and Christian 1998; White *et al.* 2006
metabolism	Amphibians	*Batrachoseps attenuatus*	*NA*	0.52	0.06	0.001	7	4	20	0.97	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Arthropoda	*Belba corynopus*	*NA*	0.65	NA	NA	4	4	15	1	Luxton 1975; Meehan 2006; Ehnes *et al.* 2011
metabolism	Arthropoda	*Bembidion*	*NA*	0.71	0.07	0	42	6	20	0.82	Ehnes *et al.* 2011
metabolism	Reptiles	*Blanus cinereus*	*NA*	0.49	NA	NA	3	3	15	0.89	Al-Sadoon and Spellerberg 1985*a*; White *et al.* 2006
metabolism	Reptiles	*Boa constrictor*	*NA*	0.89	NA	NA	3	3	14	1	Andrews and Pough 1985; Chappell and Ellis 1987*b*; White *et al.* 2006
metabolism	Amphibians	*Bolitoglossa occidentalis*	*NA*	0.71	0.24	0.098	5	3	20	0.81	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Bolitoglossa subpalmata*	*NA*	0.73	NA	NA	4	4	15	0.98	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Boulengerula taitanus*	*NA*	0.52	NA	NA	3	3	15	1	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Bufo americanus*	*NA*	0.39	0.18	0.076	10	6	20	0.92	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Bufo boreas*	*NA*	0.31	0.2	0.139	16	7	25	0.38	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Bufo bufo*	*NA*	0.47	0.11	0.004	9	5	19	0.77	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Bufo cognatus*	*NA*	0.46	0.14	0.042	6	6	25	0.8	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Bufo marinus*	*NA*	0.55	0.16	0.007	12	7	20	0.8	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Bufo terrestris*	*NA*	0.69	0.15	0.01	7	5	25	0.97	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Bufo woodhousii*	*NA*	0.33	0.27	0.3	6	5	15	0.62	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Reptiles	*Bunopus tuberculatus*	*NA*	0.4	NA	NA	3	3	15	0.99	Al-Sadoon and Abdo 1989; White *et al.* 2006
metabolism	Arthropoda	*Calathus fuscipes*	*NA*	0.55	0.06	0	81	6	25	0.5	Ehnes *et al.* 2011
metabolism	Arthropoda	*Calathus melanocephalus*	*NA*	0.54	0.06	0	53	6	25	0.62	Ehnes *et al.* 2011

rate type	taxonomic group	predator species	resource species	E	s.e.(E)	P-value (E)	n	temp levels	temp range	R^2	reference
metabolism	Reptiles	*Candoia carinatus*	*NA*	0.8	NA	NA	3	3	14	1	Chappell and Ellis 1987*b*; White *et al.* 2006
metabolism	Arthropoda	*Carabodes coriaceus*	*NA*	0.87	NA	NA	3	3	10	0.99	Berthet 1964; Meehan 2006; White *et al.* 2006
metabolism	Arthropoda	*Carabodes marginatus*	*NA*	0.66	NA	NA	3	3	10	0.95	Berthet 1964; Meehan 2006; White *et al.* 2006
metabolism	Arthropoda	*Carabus auratus*	*NA*	0.85	0.1	0	41	5	14	0.67	Ehnes *et al.* 2011
metabolism	Fish	*Catostomus commersonii*	*NA*	0.72	0.13	0.002	8	3	10	0.89	Bokma 2004; White *et al.* 2006
metabolism	Arthropoda	*Ceratozetes gracilis*	*NA*	0.86	0.16	0.014	6	4	15	0.9	Wood and Lawton 1973; Luxton 1975; Mitchell 1979; Meehan 2006; Ehnes *et al.* 2011
metabolism	Arthropoda	*Ceratozetes kananaskis*	*NA*	0.72	NA	NA	4	4	15	0.97	Mitchell 1979; Meehan 2006; Ehnes *et al.* 2011
metabolism	Fish	*Chaenocephalus aceratus*	*NA*	-0.13	NA	NA	17	4	6	0.06	Bokma 2004; White *et al.* 2006
metabolism	Reptiles	*Chalcides ocellatus*	*NA*	0.46	NA	NA	8	8	30	0.98	Al-Sadoon and Spellerberg 1985*a*, 1987; Andrews and Pough 1985; White *et al.* 2006
metabolism	Arthropoda	*Chamobates cuspidatus*	*NA*	1.21	NA	NA	3	3	10	1	Berthet 1964; Meehan 2006; White *et al.* 2006
metabolism	Reptiles	*Chelydra serpentina*	*NA*	0.88	NA	NA	3	3	20	1	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Fish	*Cirrhinus cirrhosus*	*NA*	0.84	0.21	0.002	14	3	10.5	0.98	Bokma 2004; White *et al.* 2006
metabolism	Reptiles	*Cnemidophorus tigris*	*NA*	0.67	NA	NA	3	3	17	1	Andrews and Pough 1985; White *et al.* 2006
metabolism	Reptiles	*Corallus caninus*	*NA*	0.77	NA	NA	3	3	14	0.99	Chappell and Ellis 1987*b*; White *et al.* 2006
metabolism	Reptiles	*Corallus enhydris*	*NA*	0.68	NA	NA	3	3	14	1	Chappell and Ellis 1987*b*; White *et al.* 2006
metabolism	Amphibians	*Crinia parinsignifera*	*NA*	0.54	0.03	0	7	7	30	0.99	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Crinia signifera*	*NA*	0.57	0.05	0	10	7	30	0.96	Gatten Jr. *et al.* 1992; White *et al.* 2006

rate type	taxonomic group	predator species	resource species	E	s.e.(E)	P-value (E)	n	temp levels	temp range	R^2	reference
metabolism	Reptiles	*Crotaphytus collaris*	*NA*	0.58	NA	NA	3	3	17	1	Andrews and Pough 1985; White *et al.* 2006
metabolism	Amphibians	*Cryptobranchus alleganiensis*	*NA*	0.61	NA	NA	3	3	20	1	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Arthropoda	*Cryptopygus antarcticus*	*NA*	0.39	0.18	0.03	46	6	20	0.45	Block and Tilbrook 1975; Procter and Bliss 1977; Block and Tilbrook 1978; Block 1979; Caruso *et al.* 2010; Ehnes *et al.* 2011
metabolism	Fish	*Cyprinus carpio carpio*	*NA*	0.37	0.1	0.001	24	7	25	0.93	Bokma 2004; White *et al.* 2006
metabolism	Arthropoda	*Damaeus clavipes*	*NA*	0.68	0.1	0.02	5	4	15	0.96	Wood and Lawton 1973; Luxton 1975; Meehan 2006; Ehnes *et al.* 2011
metabolism	Fish	*Dasyatis sabina*	*NA*	0.27	0.63	0.678	10	8	2.7	0.84	Bokma 2004; White *et al.* 2006
metabolism	Annelida	*Dendrobaena veneta*	*NA*	0.41	0.06	0	35	8	21.3	0.63	Ehnes *et al.* 2011
metabolism	Amphibians	*Desmognathus fuscus*	*NA*	0.36	0.16	0.047	14	7	15	0.77	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Desmognathus ochrophaes*	*NA*	0.59	0.1	0	19	7	16	0.82	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Desmognathus quadramaculatus*	*NA*	0.41	0.12	0.005	15	5	20	0.65	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Arthropoda	*Dicyrtomina minuta*	*NA*	0.93	0.13	0.086	4	4	9	0.98	Zinkler 1966; Petersen 1981; Meehan 2006; Ehnes *et al.* 2011
metabolism	Reptiles	*Diplometopon zarudnyi*	*NA*	0.4	NA	NA	6	6	25	0.93	Al-Sadoon 1986; White *et al.* 2006
metabolism	Reptiles	*Dipsosaurus dorsalis*	*NA*	0.63	NA	NA	7	7	25	0.96	Bennett and Dawson 1972; Andrews and Pough 1985; White *et al.* 2006
metabolism	Annelida	*Eisenia foetida*	*NA*	0.52	0.05	0	46	18	31	0.87	Knoz 1957; Byzova 1965; Mitchell 1979; Meehan 2006; Ehnes *et al.* 2011

rate type	taxonomic group	predator species	resource species	E	s.e.(E)	P-value (E)	n	temp levels	temp range	R^2	reference
metabolism	Annelida	*Eiseniella tetraedra*	*NA*	0.47	0.14	0.018	8	8	18	0.71	Knoz 1957; Byzova 1965; Meehan 2006; Ehnes *et al.* 2011
metabolism	Amphibians	*Ensatina eschscholtzi*	*NA*	0.49	NA	NA	3	3	11	1	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Reptiles	*Epicrates cenchria*	*NA*	0.73	NA	NA	3	3	14	0.99	Chappell and Ellis 1987*b*; White *et al.* 2006
metabolism	Arthropoda	*Ereynetes macquariensis*	*NA*	0.23	0.09	0.234	4	3	10	0.95	Goddard 1977*b*; Caruso *et al.* 2010; Ehnes *et al.* 2011
metabolism	Reptiles	*Eryx colubrinus*	*NA*	0.74	NA	NA	3	3	14	1	Chappell and Ellis 1987*b*; White *et al.* 2006
metabolism	Reptiles	*Eumeces obsoletus*	*NA*	0.89	NA	NA	3	3	17	1	Andrews and Pough 1985; White *et al.* 2006
metabolism	Amphibians	*Eurycea bislineata*	*NA*	0.61	0.15	0.015	7	6	19	0.81	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Eurycea multiplicata*	*NA*	0.48	0.33	0.199	9	5	20	0.56	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Arthropoda	*Euzetes globulus*	*NA*	0.93	0.08	0	7	6	25	0.97	Berthet 1964; Zinkler 1966; Wood and Lawton 1973; Meehan 2006; Ehnes *et al.* 2011
metabolism	Fish	*Exodon paradoxus*	*NA*	0.85	NA	NA	3	3	10	1	Bokma 2004; White *et al.* 2006
metabolism	Arthropoda	*Folsomia manolachei*	*NA*	1.77	NA	NA	3	3	9	1	Petersen 1981; Meehan 2006; Ehnes *et al.* 2011
metabolism	Arthropoda	*Folsomia quadrioculata*	*NA*	0.76	NA	NA	6	3	9	0.95	Petersen 1981; Meehan 2006; Ehnes *et al.* 2011
metabolism	Fish	*Gadus morhua*	*NA*	0.41	0.12	0.002	51	5	10	0.96	Bokma 2004; White *et al.* 2006
metabolism	Arthropoda	*Gamasellus racovitzai*	*NA*	0.48	0.09	0	18	3	10	0.94	Goddard 1977*a*; Caruso *et al.* 2010; Ehnes *et al.* 2011
metabolism	Fish	*Gambusia affinis*	*NA*	0.39	NA	NA	3	3	10	1	Bokma 2004; White *et al.* 2006

rate type	taxonomic group	predator species	resource species	E	s.e.(E)	P-value (E)	n	temp levels	temp range	R^2	reference
metabolism	Arthropoda	*Geolycosa domifex*	*NA*	1.22	NA	NA	3	3	7	0.91	Anderson 1970; Moulder and Reichle 1972; Humphreys 1976; Meehan 2006; Ehnes *et al.* 2011
metabolism	Arthropoda	*Geophilidae*	*NA*	0.81	0.06	0	135	20	25	0.66	Ehnes *et al.* 2011
metabolism	Arthropoda	*Glomeris*	*NA*	0.74	0.06	0	53	10	25	0.73	Ehnes *et al.* 2011
metabolism	Annelida	*Glossoscolex paulistus*	*NA*	0.21	0.03	0.02	5	5	20	0.98	Abe 1985; Meehan 2006; Ehnes *et al.* 2011
metabolism	Amphibians	*Gyrinophilus danielsi*	*NA*	0.71	NA	NA	3	3	23	1	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Gyrinophilus porphyrictus*	*NA*	0.77	0.32	0.141	5	4	20	0.82	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Arthropoda	*Harpalus*	*NA*	0.72	0.09	0	38	6	17	0.66	Ehnes *et al.* 2011
metabolism	Reptiles	*Helicops modestus*	*NA*	0.35	NA	NA	3	3	10	0.94	Andrews and Pough 1985; White *et al.* 2006
metabolism	Reptiles	*Hemidactylus frenatus*	*NA*	0.99	0.18	0.113	4	4	10	0.98	Andrews and Pough 1985; White *et al.* 2006
metabolism	Arthropoda	*Hemileius initialis*	*NA*	0.69	NA	NA	4	4	15	1	Luxton 1975; Meehan 2006; Ehnes *et al.* 2011
metabolism	Arthropoda	*Hogna lenta*	*NA*	0.73	0.11	0.096	4	3	20	0.98	Anderson 1970; Ford 1977*b*; Greenstone and Bennett 1980; Anderson 1996; Meehan 2006; Ehnes *et al.* 2011
metabolism	Amphibians	*Hyla chrysoscelis*	*NA*	0.75	0.01	0.01	4	3	20	1	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Hyla cinerea*	*NA*	0.35	0.14	0.063	7	7	20	0.82	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Hyla gratiosa*	*NA*	0.35	0.01	0.027	4	4	24	1	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Hyla versicolor*	*NA*	0.28	0.2	0.295	5	5	20	0.5	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Arthropoda	*Hypochthonius rufulus*	*NA*	0.93	NA	NA	4	4	15	0.99	Berthet 1964; Meehan 2006; White *et al.* 2006
metabolism	Reptiles	*Iguana iguana*	*NA*	0.6	NA	NA	3	3	17	0.99	Andrews and Pough 1985; White *et al.* 2006

rate type	taxonomic group	predator species	resource species	E	s.e.(E)	P-value (E)	n	temp levels	temp range	R^2	reference
metabolism	Arthropoda	*Isopoda*	*NA*	0.25	0.07	0.003	21	4	25	0.84	Ehnes *et al.* 2011
metabolism	Arthropoda	*Isotomiella minor*	*NA*	0.56	NA	NA	3	3	9	0.95	Petersen 1981; Meehan 2006; Ehnes *et al.* 2011
metabolism	Arthropoda	*Julidae*	*NA*	0.66	0.04	0	127	17	25	0.72	Ehnes *et al.* 2011
metabolism	Reptiles	*Klauberina riversiana*	*NA*	0.84	NA	NA	3	3	10	1	Mautz 1979; Andrews and Pough 1985; White *et al.* 2006
metabolism	Reptiles	*Lacerta agilis*	*NA*	0.52	NA	NA	3	3	15	1	Al-Sadoon and Spellerberg 1985*a*; White *et al.* 2006
metabolism	Reptiles	*Lacerta vivipara*	*NA*	0.62	0.04	0	14	7	30	0.96	Al-Sadoon and Spellerberg 1985*a*; Andrews and Pough 1985; Patterson and Davies 1989; White *et al.* 2006
metabolism	Fish	*Lampetra fluviatilis*	*NA*	0.92	0.07	0	46	9	11.6	0.98	Bokma 2004; White *et al.* 2006
metabolism	Fish	*Lampetra planeri*	*NA*	0.94	NA	NA	17	7	10.3	0.39	Bokma 2004; White *et al.* 2006
metabolism	Reptiles	*Lampropeltis miliaris*	*NA*	0.64	NA	NA	3	3	10	0.99	Andrews and Pough 1985; White *et al.* 2006
metabolism	Arthropoda	*Lepidocyrtus*	*NA*	0.69	NA	NA	3	3	9	0.87	Petersen 1981; Meehan 2006; Ehnes *et al.* 2011
metabolism	Reptiles	*Lepidophyma gaigeae*	*NA*	0.75	NA	NA	4	4	15	0.96	Mautz 1979; Andrews and Pough 1985; White *et al.* 2006
metabolism	Reptiles	*Lepidophyma smithi*	*NA*	0.63	NA	NA	3	3	10	0.99	Mautz 1979; Andrews and Pough 1985; White *et al.* 2006
metabolism	Arthropoda	*Liacarus coracinus*	*NA*	0.9	NA	NA	3	3	10	0.96	Berthet 1964; Meehan 2006; White *et al.* 2006
metabolism	Reptiles	*Liasis fuscus*	*NA*	0.88	NA	NA	4	4	9	0.93	Bedford and Christian 1998; White *et al.* 2006
metabolism	Reptiles	*Liasis olivaceus*	*NA*	0.67	0.23	0.207	4	4	9	0.93	Bedford and Christian 1998; White *et al.* 2006
metabolism	Reptiles	*Lichanura trivirgata*	*NA*	0.78	NA	NA	3	3	14	0.99	Chappell and Ellis 1987*b*; White *et al.* 2006

rate type	taxonomic group	predator species	resource species	E	s.e.(E)	P-value (E)	n	temp levels	temp range	R^2	reference
metabolism	Fish	*Limanda limanda*	*NA*	0.71	NA	NA	3	3	10	1	Bokma 2004; White *et al.* 2006
metabolism	Arthropoda	*Lithobius forficatus*	*NA*	0.78	0.04	0	252	17	26	0.74	Ehnes *et al.* 2011
metabolism	Arthropoda	*Loricera pilicornis*	*NA*	0.67	0.04	0	49	6	25	0.84	Ehnes *et al.* 2011
metabolism	Annelida	*Lumbricus castaneus*	*NA*	0.13	0.09	0.235	7	7	15	0.91	Gromadska 1962; Byzova 1965; Meehan 2006; Ehnes *et al.* 2011
metabolism	Annelida	*Lumbricus terrestris*	*NA*	0.35	0.04	0	74	11	21.3	0.95	Byzova 1965; Fitzpatrick *et al.* 1987; Meehan 2006; Ehnes *et al.* 2011
metabolism	Arthropoda	*Lycosa godeffroyi*	*NA*	0.41	NA	NA	8	6	36	0.74	Anderson 1996; Meehan 2006; Ehnes *et al.* 2011
metabolism	Arthropoda	*Lycosidae*	*NA*	0.37	NA	NA	3	3	10	1	Reichle 1968; Hadley *et al.* 1981; Anderson and Prestwich 1982; Meehan 2006; Ehnes *et al.* 2011
metabolism	Annelida	*Megascolex mauritii*	*NA*	0.4	0.02	0	79	5	20	0.91	Saroja 1959; Ehnes *et al.* 2011
metabolism	Fish	*Micropterus salmoides*	*NA*	0.45	0.09	0.007	7	4	15	0.99	Bokma 2004; White *et al.* 2006
metabolism	Fish	*Microstomus kitt*	*NA*	0.36	NA	NA	3	3	10	1	Bokma 2004; White *et al.* 2006
metabolism	Reptiles	*Morelia spilota*	*NA*	0.81	NA	NA	3	3	14	1	Chappell and Ellis 1987*b*; White *et al.* 2006
metabolism	Reptiles	*Morelia spilota spilota*	*NA*	0.56	NA	NA	4	4	9	0.86	Bedford and Christian 1998; White *et al.* 2006
metabolism	Reptiles	*Morelia spilota variegata*	*NA*	-0.36	0.07	0.125	4	4	9	1	Bedford and Christian 1998; White *et al.* 2006
metabolism	Fish	*Mugil cephalus*	*NA*	0.66	0.07	0	18	9	14	0.88	Bokma 2004; White *et al.* 2006
metabolism	Arthropoda	*Nanhermannia elegantula*	*NA*	0.97	NA	NA	3	3	10	0.97	Berthet 1964; Meehan 2006; White *et al.* 2006
metabolism	Arthropoda	*Nanorchestes antarcticus*	*NA*	0.73	0.82	0.39	15	3	10	0.58	Block 1976; Meehan 2006; Ehnes *et al.* 2011
metabolism	Reptiles	*Natrix maura*	*NA*	0.71	NA	NA	6	6	30	1	Hailey and Davies 1986; White *et al.* 2006

rate type	taxonomic group	predator species	resource species	E	s.e.(E)	P-value (E)	n	temp levels	temp range	R^2	reference
metabolism	Reptiles	*Natrix natrix helretica*	*NA*	0.91	NA	NA	7	7	30	0.98	Hailey and Davies 1986; White *et al.* 2006
metabolism	Reptiles	*Natrix natrix persa*	*NA*	0.74	NA	NA	7	7	30	0.99	Hailey and Davies 1986; White *et al.* 2006
metabolism	Arthropoda	*Nebria brevicollis*	*NA*	0.26	0.06	0	67	6	25	0.39	Ehnes *et al.* 2011
metabolism	Amphibians	*Necturus maculosus*	*NA*	0.65	0.14	0.004	9	6	20	0.8	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Arthropoda	*Nemobius silvestris*	*NA*	0.62	0.52	0.255	13	8	3	0.89	Krüger 1958; Ehnes *et al.* 2011
metabolism	Arthropoda	*Nothrus silvestris*	*NA*	0.98	0.17	0	15	4	15	0.86	Berthet 1964; Webb 1969; Thomas 1979; Meehan 2006; Ehnes *et al.* 2011
metabolism	Arthropoda	*Notiophilus*	*NA*	0.94	0.19	0	24	5	14	0.56	Ehnes *et al.* 2011
metabolism	Amphibians	*Notophthalmus viridescens*	*NA*	0.14	0.16	0.395	9	5	20	0.22	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Occidozyga martensii*	*NA*	0.38	NA	NA	5	5	20	0.92	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Arthropoda	*Ocypus ophtalmicus*	*NA*	0.85	0.06	0	32	5	20	0.89	Ehnes *et al.* 2011
metabolism	Fish	*Oncorhynchus mykiss*	*NA*	0.49	0.05	0	81	16	21	0.91	Bokma 2004; White *et al.* 2006
metabolism	Fish	*Oncorhynchus nerka*	*NA*	0.52	0.12	0.002	12	6	20	0.97	Bokma 2004; White *et al.* 2006
metabolism	Arthropoda	*Oniscus asellus*	*NA*	0.71	0.06	0	68	16	25	0.79	Phillipson and Watson 1965; Meehan 2006; Ehnes *et al.* 2011
metabolism	Fish	*Ophiodon elongatus*	*NA*	0.74	0.63	0.269	14	9	3.2	0.93	Bokma 2004; White *et al.* 2006
metabolism	Arthropoda	*Oppia nova*	*NA*	0.92	NA	NA	3	3	10	0.87	Berthet 1964; Meehan 2006; White *et al.* 2006
metabolism	Arthropoda	*Oppia subpectinata*	*NA*	0.9	NA	NA	3	3	10	1	Berthet 1964; Meehan 2006; White *et al.* 2006
metabolism	Arthropoda	*Oribatella quadricornuta*	*NA*	1.16	NA	NA	3	3	10	1	Berthet 1964; Meehan 2006; White *et al.* 2006
metabolism	Fish	*Orthodon microlepidotus*	*NA*	0.56	0.09	0.002	8	7	20	0.88	Bokma 2004; White *et al.* 2006

rate type	taxonomic group	predator species	resource species	E	s.e.(E)	P-value (E)	n	temp levels	temp range	R^2	reference
metabolism	Arthropoda	*Parachipteria willmanni*	*NA*	1.1	0.27	0.007	9	3	10	0.87	Berthet 1964; Wood and Lawton 1973; Meehan 2006; Ehnes *et al.* 2011
metabolism	Arthropoda	*Pardosa amenatata*	*NA*	0.93	NA	NA	10	9	12	0.96	Scholander *et al.* 1953; Anderson 1970; Moeur and Eriksen 1972; Humphreys 1976; McQueen 1980; Greenstone and Bennett 1980; Kotiaho *et al.* 1998; Kotiaho 1998; Meehan 2006; Ehnes *et al.* 2011
metabolism	Arthropoda	*Pardosa astrigera*	*NA*	0.68	0.27	0.088	6	3	10	0.69	Ford 1977*b*; Meehan 2006; Ehnes *et al.* 2011
metabolism	Arthropoda	*Pardosa lugubris*	*NA*	0.7	0.07	0	50	7	21.9	0.68	Ford 1977*a*; Meehan 2006; Ehnes *et al.* 2011
metabolism	Arthropoda	*Pardosa palustris*	*NA*	0.79	0.14	0	26	5	14	0.59	Ehnes *et al.* 2011
metabolism	Arthropoda	*Parisotoma notabilis*	*NA*	0.52	NA	NA	3	3	9	0.97	Petersen 1981; Meehan 2006; Ehnes *et al.* 2011
metabolism	Fish	*Petromyzon marinus*	*NA*	0.75	0.12	0.1	4	4	15	1	Bokma 2004; White *et al.* 2006
metabolism	Arthropoda	*Phidippus regius*	*NA*	0.63	NA	NA	3	3	20	0.99	Catlett 1973; Myrcha and Stejgwillo-Laudanska 1973; Humphreys 1976; Meehan 2006; Ehnes *et al.* 2011
metabolism	Arthropoda	*Philonthus*	*NA*	0.98	0.1	0	11	4	14	0.93	Ehnes *et al.* 2011
metabolism	Reptiles	*Phrynosoma m'calli*	*NA*	0.63	NA	NA	3	3	17	1	Andrews and Pough 1985; White *et al.* 2006
metabolism	Amphibians	*Phyllomedusa sauvagei*	*NA*	0.66	NA	NA	6	6	28	1	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Reptiles	*Physignathus lesueurii*	*NA*	0.67	NA	NA	3	3	17	1	Andrews and Pough 1985; White *et al.* 2006
metabolism	Arthropoda	*Pilogalumna allifera*	*NA*	0.55	NA	NA	6	6	22	0.91	Stamou *et al.* 1995; Meehan 2006; Ehnes *et al.* 2011

rate type	taxonomic group	predator species	resource species	E	s.e.(E)	P-value (E)	n	temp levels	temp range	R^2	reference
metabolism	Arthropoda	*Pirata latitans*	*NA*	0.8	0.1	0	32	6	14	0.71	Nakamura 1972; Schmitz 2004; Meehan 2006; Ehnes *et al.* 2011
metabolism	Arthropoda	*Pisaura mirabilis*	*NA*	0.73	0.1	0	35	5	14	0.7	Ehnes *et al.* 2011
metabolism	Reptiles	*Pitupophis catenifer affinis*	*NA*	0.54	NA	NA	4	4	30	0.89	Greenwald 1971; White *et al.* 2006
metabolism	Fish	*Platichthys flesus*	*NA*	0.6	0.48	0.305	6	4	10	0.59	Bokma 2004; White *et al.* 2006
metabolism	Fish	*Platichthys stellatus*	*NA*	0.72	0.13	0	22	15	11	0.71	Bokma 2004; White *et al.* 2006
metabolism	Arthropoda	*Platynothrus peltifer*	*NA*	0.79	0.19	0.008	8	5	25	0.79	Berthet 1964; Thomas 1979; Meehan 2006; Ehnes *et al.* 2011
metabolism	Arthropoda	*Platynus dorsalis*	*NA*	0.78	0.05	0	98	10	25	0.72	Ehnes *et al.* 2011
metabolism	Amphibians	*Plethodon cinereus*	*NA*	0.42	0.05	0	14	10	20	0.91	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Plethodon dorsalis*	*NA*	-0.04	0	0.019	4	4	15	1	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Plethodon glutinosus*	*NA*	0.57	0.21	0.038	9	6	20	0.62	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Plethodon jordani*	*NA*	0.7	0.05	0	9	7	20	0.98	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Plethodon neomexicanus*	*NA*	0.17	NA	NA	5	5	20	0.89	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Fish	*Pleuronectes platessa*	*NA*	0.45	0.08	0	26	4	15	0.81	Bokma 2004; White *et al.* 2006
metabolism	Reptiles	*Podarcis hispanica*	*NA*	0.81	0.05	0	10	7	30	0.98	Al-Sadoon and Spellerberg 1985*b*; Patterson and Davies 1989; White *et al.* 2006
metabolism	Reptiles	*Podarcis muralis*	*NA*	0.52	NA	NA	3	3	15	0.84	Al-Sadoon and Spellerberg 1985*a*; White *et al.* 2006
metabolism	Arthropoda	*Poecilus versicolor*	*NA*	0.72	0.05	0	47	5	25	0.82	Ehnes *et al.* 2011
metabolism	Arthropoda	*Pogonognathellus flavescens*	*NA*	1.07	NA	NA	3	3	9	1	Zinkler 1966; Petersen 1981; Meehan 2006; Ehnes *et al.* 2011

rate type	taxonomic group	predator species	resource species	E	s.e.(E)	P-value (E)	n	temp levels	temp range	R^2	reference
metabolism	Arthropoda	*Polydesmida*	*NA*	0.33	0.19	0.101	24	3	9	0.54	Ehnes *et al.* 2011
metabolism	Arthropoda	*Porcellio laevis*	*NA*	0.78	0.2	0.004	11	7	25	0.67	Edney 1964; Lardies *et al.* 2004; Meehan 2006; Ehnes *et al.* 2011
metabolism	Arthropoda	*Porcellio scaber*	*NA*	0.85	0.1	0	59	13	24.6	0.59	?Saito 1969; Meehan 2006; Ehnes *et al.* 2011
metabolism	Arthropoda	*Porcellionides pruinosus*	*NA*	0.45	0.09	0.003	8	6	20	0.93	Reichle 1968; Cloudsley-Thompson 1969; Al-Dabbagh and Marina 1986; Meehan 2006; Ehnes *et al.* 2011
metabolism	Arthropoda	*Protaphorura armata*	*NA*	0.63	0.05	0	7	6	15	0.99	Zinkler 1966; Petersen 1981; Meehan 2006; Ehnes *et al.* 2011
metabolism	Arthropoda	*Protaphorura meridiata*	*NA*	0.22	NA	NA	5	5	20	0.89	Argyropoulou and Stamou 1993; Meehan 2006; Ehnes *et al.* 2011
metabolism	Reptiles	*Psammodromus algirus*	*NA*	0.74	NA	NA	3	3	15	1	Al-Sadoon and Spellerberg 1985*a*; White *et al.* 2006
metabolism	Amphibians	*Pseudacris triseriata*	*NA*	0.51	0.28	0.104	10	6	20	0.43	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Reptiles	*Pseudemys scripta*	*NA*	0.81	NA	NA	4	4	30	1	Gatten Jr. 1974; White *et al.* 2006
metabolism	Amphibians	*Pseudoeurycea gadovii*	*NA*	0.66	NA	NA	3	3	20	1	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Pseudoeurycea goebeli*	*NA*	0.78	NA	NA	3	3	20	1	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Reptiles	*Pseudonaja nuchalis*	*NA*	0.61	NA	NA	4	4	9	0.95	Bedford and Christian 1998; White *et al.* 2006
metabolism	Arthropoda	*Pseudophonus rufipes*	*NA*	0.63	0.05	0	96	10	25	0.65	Ehnes *et al.* 2011
metabolism	Fish	*Pseudopleuronectes americanus*	*NA*	1.22	0.15	0	56	7	19	0.72	Bokma 2004; White *et al.* 2006
metabolism	Amphibians	*Pseudotriton ruber*	*NA*	0.78	0.02	0.015	4	3	20	1	Gatten Jr. *et al.* 1992; White *et al.* 2006

rate type	taxonomic group	predator species	resource species	E	s.e.(E)	P-value (E)	n	temp levels	temp range	R^2	reference
metabolism	Arthropoda	*Pterostichus melanarius*	*NA*	0.7	0.06	0	84	7	25	0.62	Ehnes *et al.* 2011
metabolism	Arthropoda	*Pterostichus niger*	*NA*	0.66	0.07	0	36	5	20	0.8	Ehnes *et al.* 2011
metabolism	Arthropoda	*Pterostichus oblongopunctatus*	*NA*	0.66	0.07	0	70	10	25	0.62	Ehnes *et al.* 2011
metabolism	Reptiles	*Python curtis*	*NA*	0.73	NA	NA	3	3	14	1	Chappell and Ellis 1987*b*; White *et al.* 2006
metabolism	Reptiles	*Python molurus*	*NA*	0.8	NA	NA	3	3	14	1	Andrews and Pough 1985; Chappell and Ellis 1987*b*; White *et al.* 2006
metabolism	Reptiles	*Python regius*	*NA*	0.77	NA	NA	3	3	14	1	Chappell and Ellis 1987*b*; White *et al.* 2006
metabolism	Reptiles	*Python reticulatus*	*NA*	0.74	NA	NA	3	3	14	1	Chappell and Ellis 1987*b*; White *et al.* 2006
metabolism	Reptiles	*Python sebae*	*NA*	0.7	NA	NA	3	3	14	1	Chappell and Ellis 1987*b*; White *et al.* 2006
metabolism	Arthropoda	*Rabidosa rabida*	*NA*	0.65	NA	NA	3	3	10	1	Moulder and Reichle 1972; Ford 1977*b*; Schmitz 2004; Meehan 2006; Ehnes *et al.* 2011
metabolism	Amphibians	*Rana arvalis*	*NA*	0.83	NA	NA	6	6	25	1	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Rana cancrivora*	*NA*	0.7	0.06	0.008	5	4	15	0.98	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Rana catesbeiana*	*NA*	0.54	0.13	0.001	19	9	25	0.78	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Rana clamitans*	*NA*	0.58	0.12	0.04	5	5	20	0.93	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Rana erythraea*	*NA*	1.1	NA	NA	5	5	20	0.93	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Rana esculenta*	*NA*	0.57	0.22	0.019	17	10	19	0.63	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Rana pipiens*	*NA*	0.63	0.06	0	30	12	25	0.81	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Rana sylvatica*	*NA*	0.23	0.06	0.015	7	5	20	0.91	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Rana temporaria*	*NA*	0.51	0.21	0.028	20	17	25.3	0.27	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Rana virgatipes*	*NA*	0.71	NA	NA	3	3	20	1	Gatten Jr. *et al.* 1992; White *et al.* 2006

rate type	taxonomic group	predator species	resource species	E	s.e.(E)	P-value (E)	n	temp levels	temp range	R^2	reference
metabolism	Arthropoda	*Rhysotritia ardua*	*NA*	1.08	NA	NA	3	3	10	0.99	Berthet 1964; Meehan 2006; White *et al.* 2006
metabolism	Fish	*Salmo salar*	*NA*	0.59	NA	NA	3	3	12	1	Bokma 2004; White *et al.* 2006
metabolism	Arthropoda	*Salticus scenicus*	*NA*	0.61	0.1	0	31	6	14	0.57	Ito 1964; Myrcha and Stejgwillo-Laudanska 1973; Meehan 2006; Ehnes *et al.* 2011
metabolism	Fish	*Salvelinus fontinalis*	*NA*	0.51	0.05	0	64	4	15	0.98	Bokma 2004; White *et al.* 2006
metabolism	Fish	*Salvelinus namaycush*	*NA*	0.72	0.09	0	33	16	13	0.84	Bokma 2004; White *et al.* 2006
metabolism	Reptiles	*Sauromalus hispidus*	*NA*	0.71	NA	NA	9	7	25	0.99	Bennett and Dawson 1972; Andrews and Pough 1985; White *et al.* 2006
metabolism	Reptiles	*Sceloporus graciosus*	*NA*	0.91	NA	NA	3	3	12	1	Andrews and Pough 1985; White *et al.* 2006
metabolism	Reptiles	*Sceloporus occidentalis*	*NA*	0.87	NA	NA	7	7	25	0.37	Dawson and Bartholomew 1956; Francis and Brooks 1970; Bennett *et al.* 1975; Gleeson 1979; Tsuji 1988; White *et al.* 2006
metabolism	Reptiles	*Sceloporus olivaceus*	*NA*	1.58	NA	NA	3	3	10	1	Andrews and Pough 1985; White *et al.* 2006
metabolism	Reptiles	*Sceloporus undulatus*	*NA*	1.16	NA	NA	4	4	15	0.95	Andrews and Pough 1985; White *et al.* 2006
metabolism	Reptiles	*Sceloporus variabilis*	*NA*	0.71	NA	NA	3	3	25	1	Tsuji 1988
metabolism	Arthropoda	*Scheloribates cf. latipes*	*NA*	0.49	NA	NA	6	6	22	0.83	Stamou *et al.* 1995; Meehan 2006; Ehnes *et al.* 2011
metabolism	Reptiles	*Scinus mitranus*	*NA*	0.55	NA	NA	6	6	25	0.96	Al-Sadoon 1986
metabolism	Fish	*Scyliorhinus canicula*	*NA*	0.49	0.08	0	22	4	10	0.83	Bokma 2004; White *et al.* 2006
metabolism	Fish	*Scyliorhinus stellaris*	*NA*	-1.89	1.3	0.22	7	5	3	0.8	Bokma 2004; White *et al.* 2006

rate type	taxonomic group	predator species	resource species	E	s.e.(E)	P-value (E)	n	temp levels	temp range	R^2	reference
metabolism	Fish	*Sebastes diploproa*	*NA*	0.36	NA	NA	9	3	10	0.74	Bokma 2004; White *et al.* 2006
metabolism	Amphibians	*Siren lacertina*	*NA*	0.57	0.25	0.066	9	5	20	0.72	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Arthropoda	*Sminthurinus*	*NA*	0.61	NA	NA	3	3	9	0.92	Petersen 1981; Meehan 2006; Ehnes *et al.* 2011
metabolism	Arthropoda	*Sminthurus viridis*	*NA*	0.52	NA	NA	4	4	25	1	Zinkler 1966; Meehan 2006; Ehnes *et al.* 2011
metabolism	Reptiles	*Spalerosophis cliffordi*	*NA*	0.66	0.06	0	9	8	26.8	0.95	Dmi'el and Borut 1972; Andrews and Pough 1985; White *et al.* 2006
metabolism	Fish	*Squalus acanthias*	*NA*	1.33	0.27	0	20	4	4	0.93	Bokma 2004; White *et al.* 2006
metabolism	Arthropoda	*Steganacarus magnus*	*NA*	0.69	0.08	0	24	8	25	0.86	Berthet 1964; Webb and Elmes 1972; Wood and Lawton 1973; Luxton 1975; Webb 1975; Meehan 2006; Ehnes *et al.* 2011
metabolism	Arthropoda	*Steganacarus spinosus*	*NA*	0.42	NA	NA	4	4	15	0.94	Luxton 1975; Meehan 2006; Ehnes *et al.* 2011
metabolism	Arthropoda	*Stereotydeus villosus*	*NA*	0.7	0.18	0.009	9	3	10	0.87	Goddard 1977*b*; Caruso *et al.* 2010; Ehnes *et al.* 2011
metabolism	Arthropoda	*Supraphorura furcifera*	*NA*	0.71	NA	NA	3	3	9	0.95	Petersen 1981; Meehan 2006; Ehnes *et al.* 2011
metabolism	Reptiles	*Tarentola mauritanica*	*NA*	0.51	NA	NA	3	3	15	1	Al-Sadoon and Spellerberg 1985*a*; White *et al.* 2006
metabolism	Amphibians	*Taricha granulosa*	*NA*	0.54	0.09	0	13	5	20	0.86	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Amphibians	*Taricha torosa*	*NA*	0.61	0.15	0.001	16	5	15	0.73	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Arthropoda	*Tectocepheus velatus*	*NA*	0.97	NA	NA	3	3	10	1	Berthet 1964; Meehan 2006; White *et al.* 2006

rate type	taxonomic group	predator species	resource species	E	s.e.(E)	P-value (E)	n	temp levels	temp range	R^2	reference
metabolism	Arthropoda	*Tenuiphantes zimmernanni*	*NA*	0.55	NA	NA	11	9	12	0.98	Anderson 1970; Hagstrum 1970; Moulder and Reichle 1972; Humphreys 1976; McQueen 1980; Anderson and Prestwich 1982; Anderson 1996; Meehan 2006; Ehnes *et al.* 2011
metabolism	Reptiles	*Terrapene ornata ornata*	*NA*	1.12	NA	NA	4	4	30	0.95	Gatten Jr. 1974; White *et al.* 2006
metabolism	unicells	*Tetrahymena pyriformis*	*NA*	0.96	NA	NA	NA	3	11.5	2	Laybourn and Finlay 1976
metabolism	unicells	*Tetrahymena pyriformis*	*NA*	0.32	NA	NA	NA	3	11.5	2	Laybourn and Finlay 1976
metabolism	Arthropoda	*Tetrodontophora bielanensis*	*NA*	0.64	0.01	0.011	4	3	15	1	Zinkler 1966; Meehan 2006; Ehnes *et al.* 2011
metabolism	Reptiles	*Thamnophis sirtalis parietalis*	*NA*	0.58	NA	NA	6	6	25	0.92	Aleksiuk 1970; White *et al.* 2006
metabolism	Reptiles	*Thamnophis sirtalis sirtalis*	*NA*	0.6	NA	NA	5	5	20	0.99	Aleksiuk 1970; White *et al.* 2006
metabolism	Amphibians	*Thorius sp.*	*NA*	0.58	NA	NA	3	3	20	1	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Fish	*Thymallus arcticus arcticus*	*NA*	0.43	NA	NA	4	4	8	0.87	Bokma 2004; White *et al.* 2006
metabolism	Arthropoda	*Trachelipus rathkii*	*NA*	0.77	0.17	0.001	13	3	10	0.68	Ehnes *et al.* 2011
metabolism	Reptiles	*Trachydosaurus rugosus*	*NA*	0.72	NA	NA	3	3	17	0.98	Andrews and Pough 1985; White *et al.* 2006
metabolism	Arthropoda	*Trichoniscus pusillus*	*NA*	0.62	NA	NA	3	3	10	1	Meyer and Phillipson 1983; Meehan 2006; Ehnes *et al.* 2011
metabolism	Amphibians	*Triturus vulgaris*	*NA*	0.24	NA	NA	3	3	19	0.69	Gatten Jr. *et al.* 1992; White *et al.* 2006
metabolism	Arthropoda	*Trochosa*	*NA*	0.65	0.05	0	53	6	18.5	0.89	Ehnes *et al.* 2011

rate type	taxonomic group	predator species	resource species	E	s.e.(E)	P-value (E)	n	temp levels	temp range	R^2	reference
metabolism	Arthropoda	*Tydeus tilbrooki*	*NA*	0.43	0.14	0.086	5	3	10	0.96	Goddard 1977*b*; Caruso *et al.* 2010; Ehnes *et al.* 2011
metabolism	Reptiles	*Uromastyx microlepis*	*NA*	0.84	0.08	0.008	5	5	20	0.98	Zari 1991; White *et al.* 2006
metabolism	Reptiles	*Uta mearnsi*	*NA*	0.88	NA	NA	3	3	17	0.96	Andrews and Pough 1985; White *et al.* 2006
metabolism	Reptiles	*Uta stansburiana*	*NA*	0.72	NA	NA	4	4	20	0.95	Dawson and Bartholomew 1956; Andrews and Pough 1985; White *et al.* 2006
metabolism	Reptiles	*Varanus exanthematicus*	*NA*	1	NA	NA	3	3	10	0.97	Wood *et al.* 1978; White *et al.* 2006
metabolism	Reptiles	*Varanus gouldi*	*NA*	0.72	NA	NA	3	3	17	0.97	Andrews and Pough 1985; White *et al.* 2006
metabolism	Reptiles	*Varanus gouldii*	*NA*	0.72	0.07	0	11	9	25	0.96	Bennett and Dawson 1972; Thompson and Withers 1992; Christian and Conley 1994; White *et al.* 2006
metabolism	Reptiles	*Varanus panoptes*	*NA*	0.82	0.08	0.01	5	5	19.5	0.98	Thompson and Withers 1992; Christian and Conley 1994
metabolism	Reptiles	*Xantusia henshawi*	*NA*	0.56	NA	NA	3	3	10	1	Mautz 1979; Andrews and Pough 1985; White *et al.* 2006
metabolism	Arthropoda	*Xenillus tegeocranus*	*NA*	0.77	NA	NA	4	4	15	1	Luxton 1975; Meehan 2006; Ehnes *et al.* 2011
metabolism	Amphibians	*Xenopus laevis*	*NA*	0.39	0.14	0.019	15	7	10	0.59	Gatten Jr. *et al.* 1992; White *et al.* 2006

Interactive effects of shifting body size and feeding adaptation drive interaction strengths of protist predators under warming

Methods

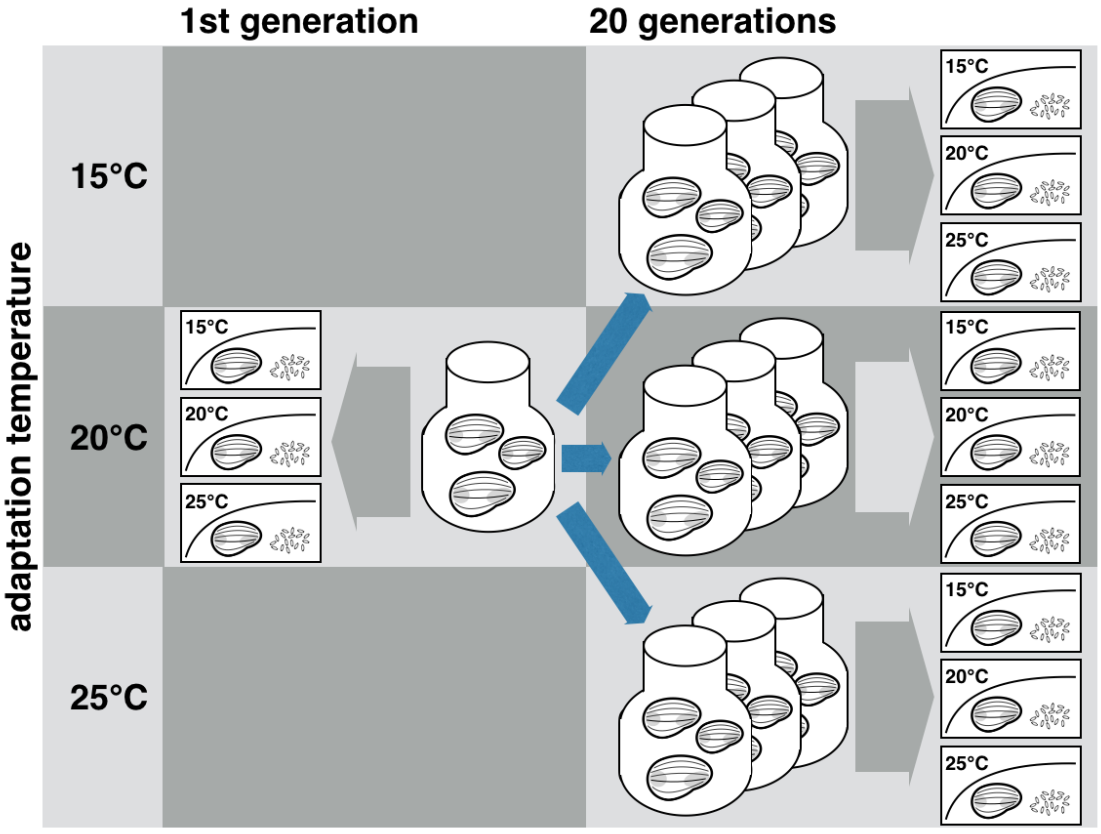

Figure 7 – Experimental design of adaptation experiment. One culture of the predatory ciliate *Tetrahymena pyriformis* was split into three times three culture which were incubated at 15° C, 20° C and 25° C respectively for 20 generations before running functional response experiments with all cultures on the non-toxic *Pseudomonas fluorescens* strain CHA-19 gfp along the full experimental temperature gradient from 15° C to 20° C and 25° C.

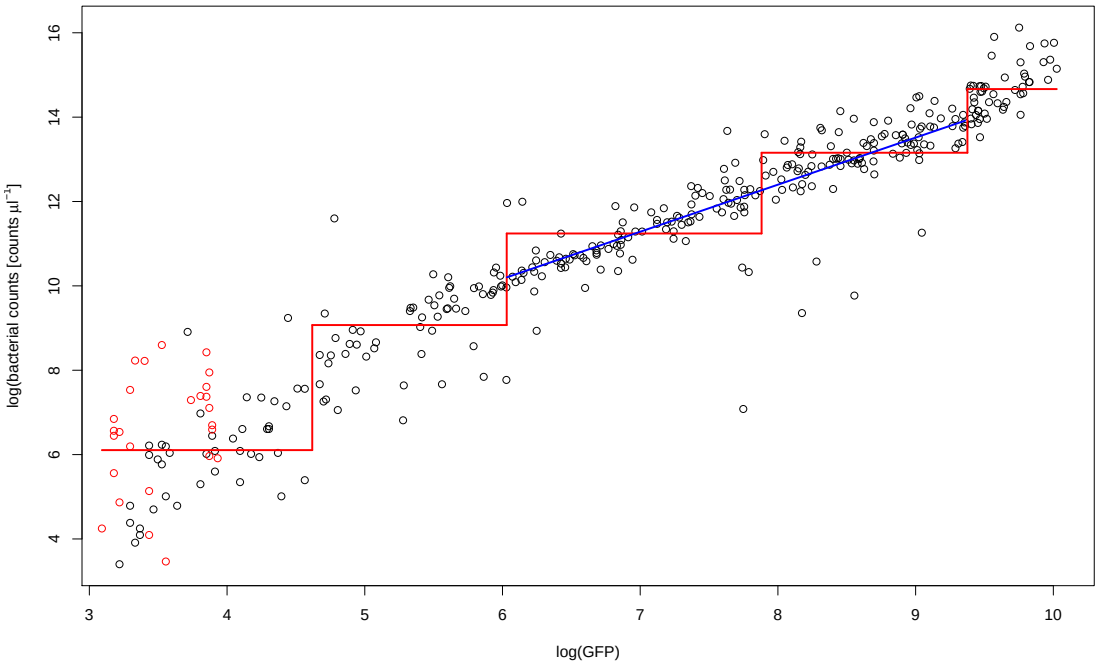

Figure 8 – ***Treemodel* analysis of fluorescent raw data:** The GFP signal measured in experimental treatments measured in a Tecan plate reader was plotted against the reference counts measured in an accuri C6 flow cytometer on a natural logarithmic scale. The treemodel (red lines) in the statistical program R was applied to select a representative area of measurements (blue line) where count data and fluorescent signal are proportional. The slope within this range was then used to transform the measured GFP signal in functional response treatments into bacterial counts.

Table 5 – **Number of experimental treatments** run at 15° C, 20° C and 25° C experimental temperatures for control treatments containing only bacterial prey but no predators, and functional response treatments for predators adapted to 15° C, 20° C and 25° C adaptation temperature for approximately 20 generations.

adaptation temperature	experimental temperature 15° C	experimental temperature 20° C	experimental temperature 25° C
control	47	47	47
15° C	36	29	27
20° C	45	37	30
25° C	43	35	24

Model analysis

Table 6 – **Model comparison of functional response models** WAIC scores (smallest indicates best model) and their standard errors. Further, direct comparison of differences in out-of-sample predictive accuracy ($elpd = -0.5 * WAIC$) to model 3 and their standard errors.

	WAIC	se_{WAIC}	$elpd_{diff}$	$se_{elpd_{diff}}$
model 1	-717.1	60.5	84.2	21.1
model 2	-832.9	56.0	26.3	18.5
model 3	-885.6	63.5	0.0	0.0
model 4	-870.1	59.4	7.7	14.9
model 5	-878.4	64.3	3.6	2.0

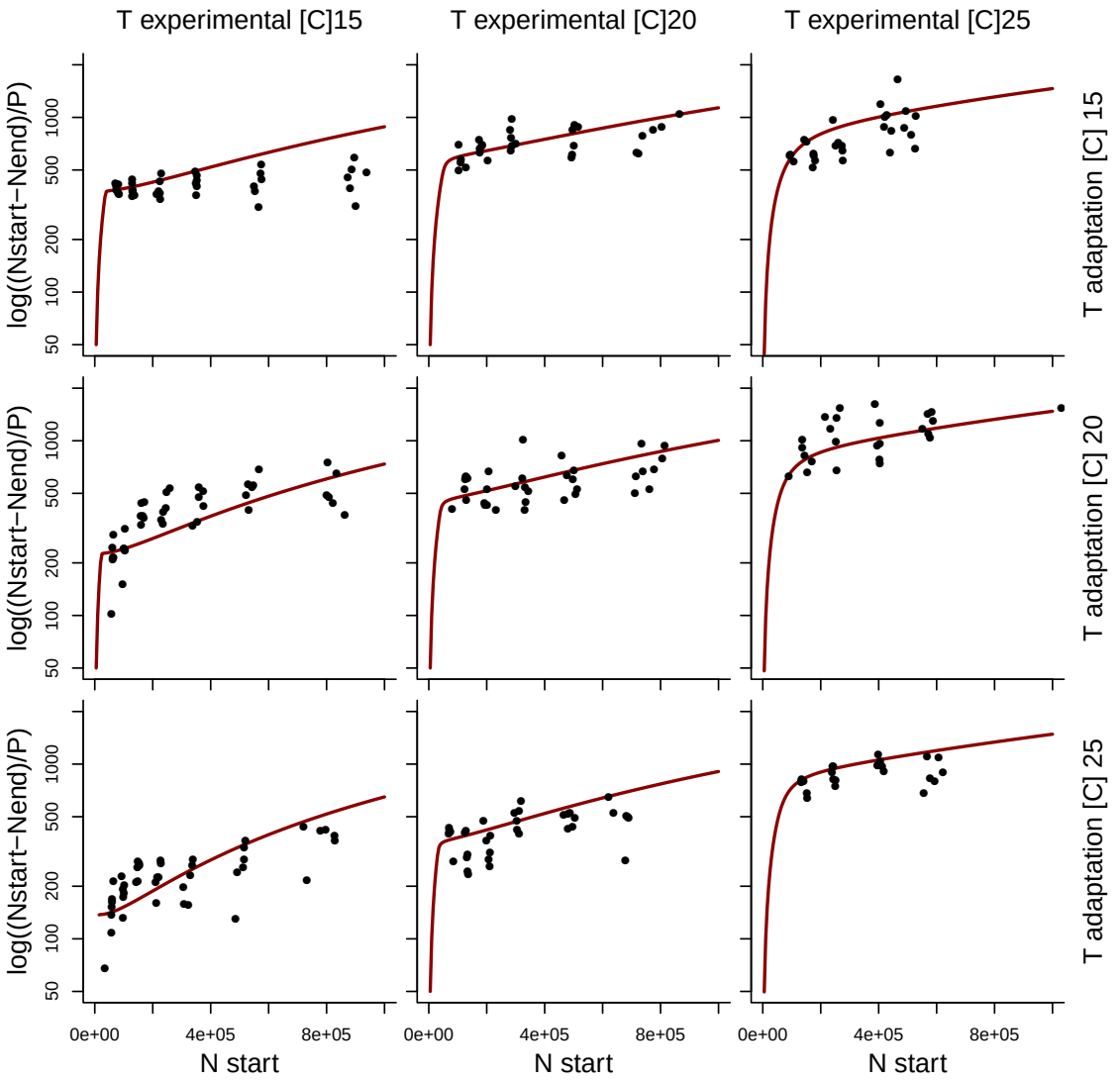

Figure 9 – **Regression of the ordinary differential equation** (Equation 3.3) of model 3 plotted with the collected functional response data. N_{end} includes prey organisms that died through feeding, as well as naturally occurring prey death.

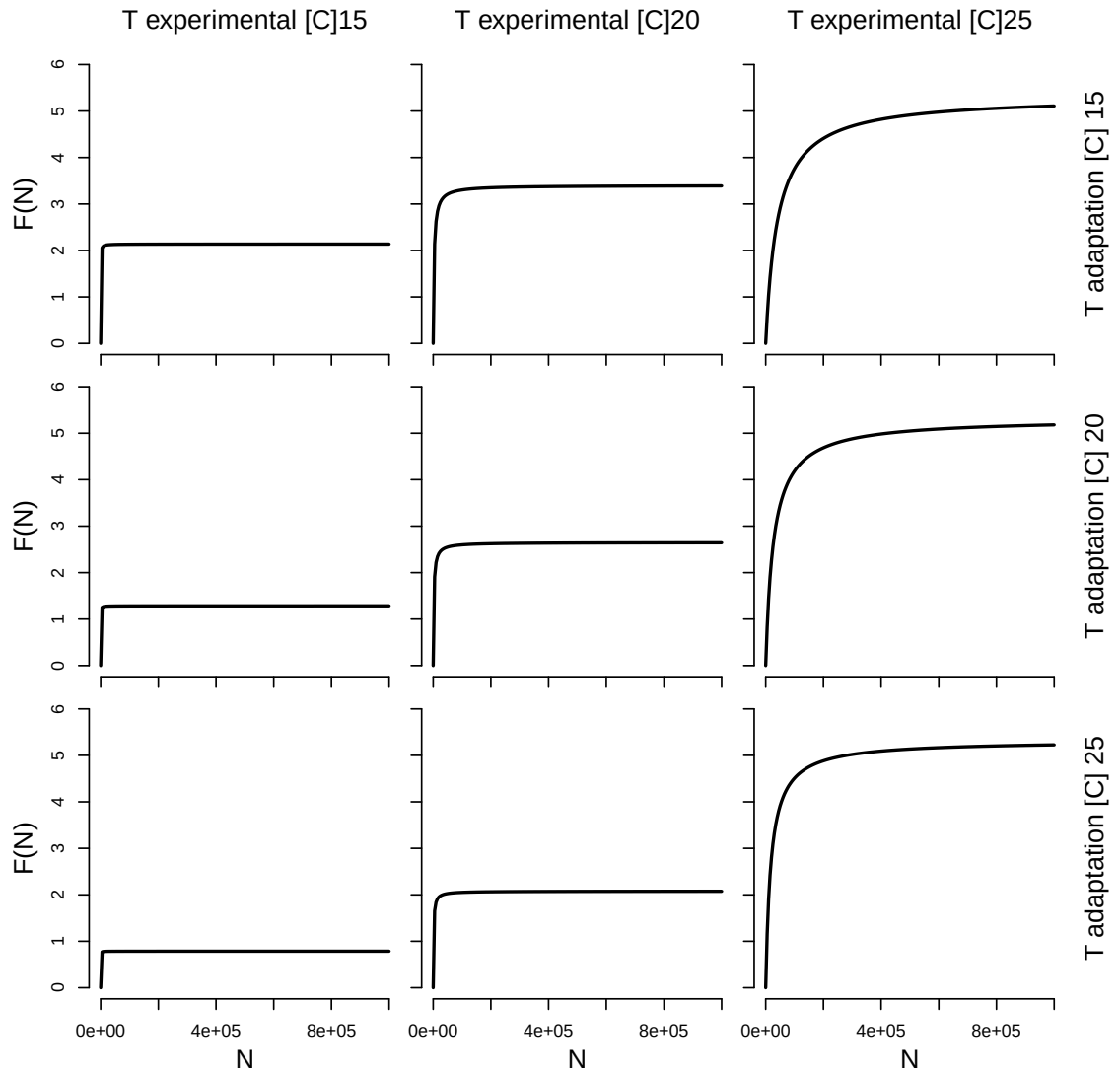

Figure 10 – **Functional response** (Equation 3.1) of model 3 at 15° C, 20° C and 25° C experimental temperature for predators adapted to 15° C, 20° C and 25° C.

Table 7 – Summary table of model 3 showing the samples from the posterior distribution showing the mean values, standard deviations and quantiles of the normalisation constants of growth rate r_0 and carrying capacity K_0 and their activation energies E_r and E_K. Further the normalisation constants of maximum feeding rate f_0 and half-saturation density η_0 and their activation energy main effects of experimental temperature E_f, E_η, of adaptive temperature A_f, A_η, and the interaction term for maximum feeding rate I_f.

	mean	se_{mean}	sd	2.5 %	25 %	50 %	75 %	97.5 %	n_{eff}	Rhat
r_0	0.001	0.000	0.000	0.001	0.001	0.001	0.000	0.000	37740	1.000
E_r	-0.012	0.002	0.384	-0.765	-0.262	-0.017	0.235	0.759	37783	1.000
K_0	39010.055	107.341	21721.214	5360.918	22575.182	36483.068	52576.252	87620.934	40949	1.000
E_K	-0.361	0.000	0.961	-2.298	-0.921	-0.363	0.194	1.599	30827	1.000
f_0	2.654	0.0005	0.085	2.505	2.595	2.647	2.706	2.841	35940	1.000
η_0	2378.247	11.130	1932.152	83.463	869.841	1930.298	3415.313	7115.469	30139	1.000
E_f	1.054	0.000	0.056	0.950	1.015	1.052	1.089	1.168	43019	1.000
E_η	4.359	0.012	1.698	2.179	3.158	3.976	5.157	8.680	20987	1.000
A_f	-0.362	0.000	0.053	-0.463	-0.398	-0.364	-0.327	-0.252	24702	1.000
A_η	-0.530	0.004	0.627	-1.531	-0.999	-0.617	-0.126	0.860	22129	1.000
I_f	0.569	0.001	0.122	0.380	0.481	0.548	0.639	0.855	21967	1.000
$sdev$	0.087	0.000	0.003	0.081	0.085	0.087	0.089	0.093	77908	1.000

Density distributions

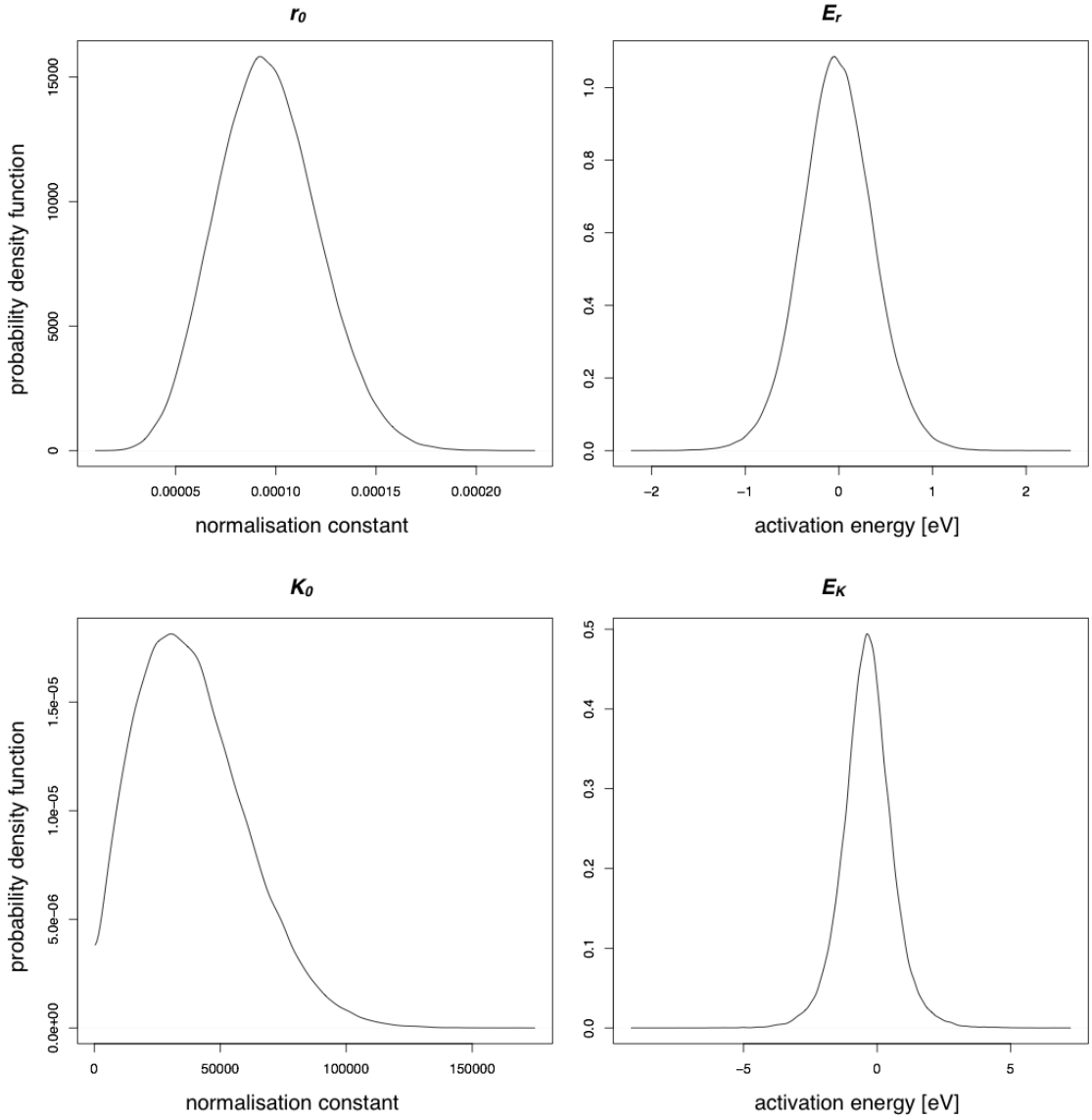

Figure 11 – **Marginal density plots** of the samples from the posterior distribution for maximum growth rate r_0 and carrying capacity K_0 parameters for the bacterial prey *Pseudomonas fluorescens* CHA19-gfp in functional response experiments.

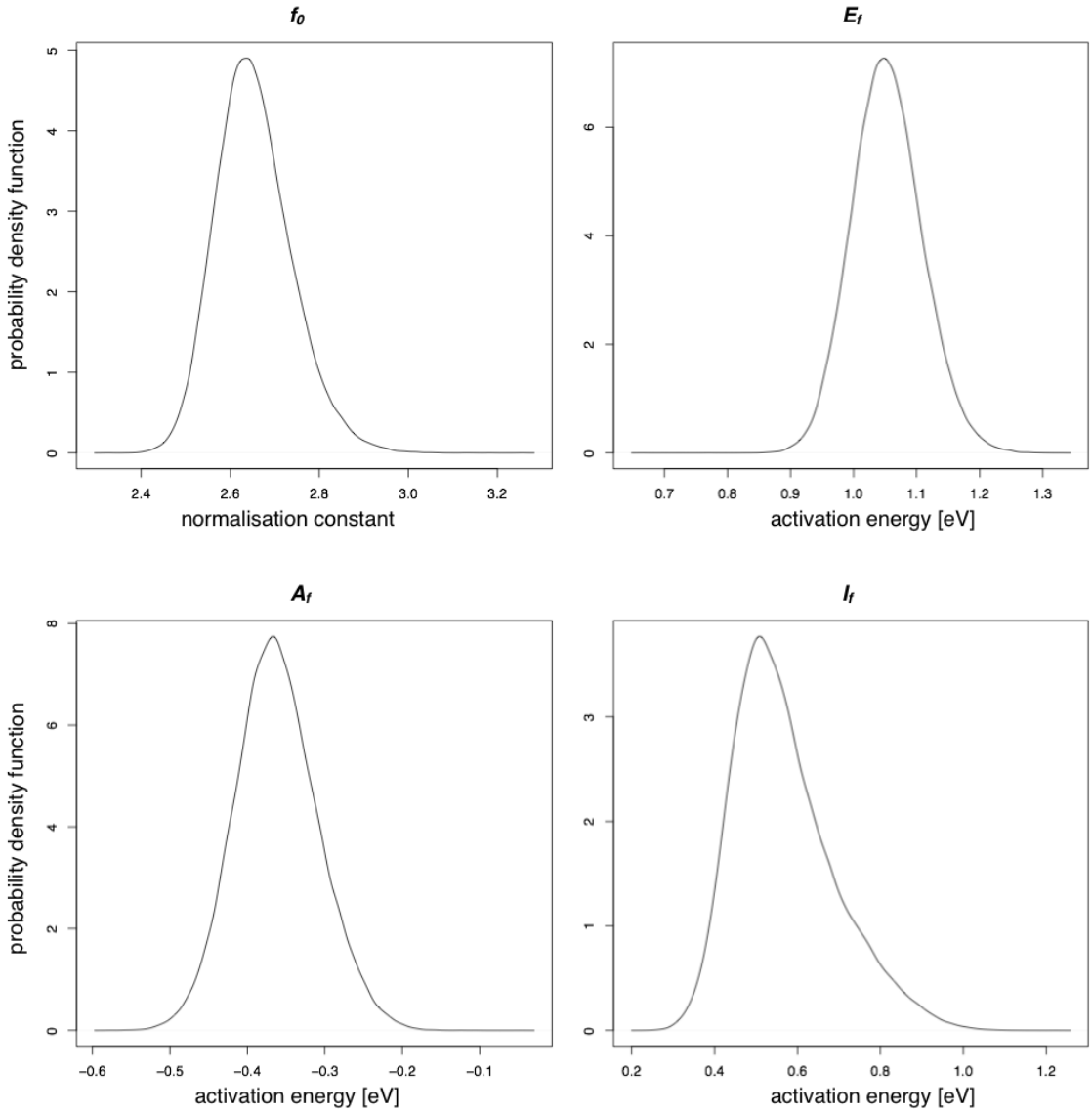

Figure 12 – **Marginal density plots** of the samples from the posterior distribution for the normalisation constant of maximum feeding rate f_0 and, the maximum feeding activation energy main effects of experimental temperature E_f, temperature adaptation A_f and interaction effect I_f.

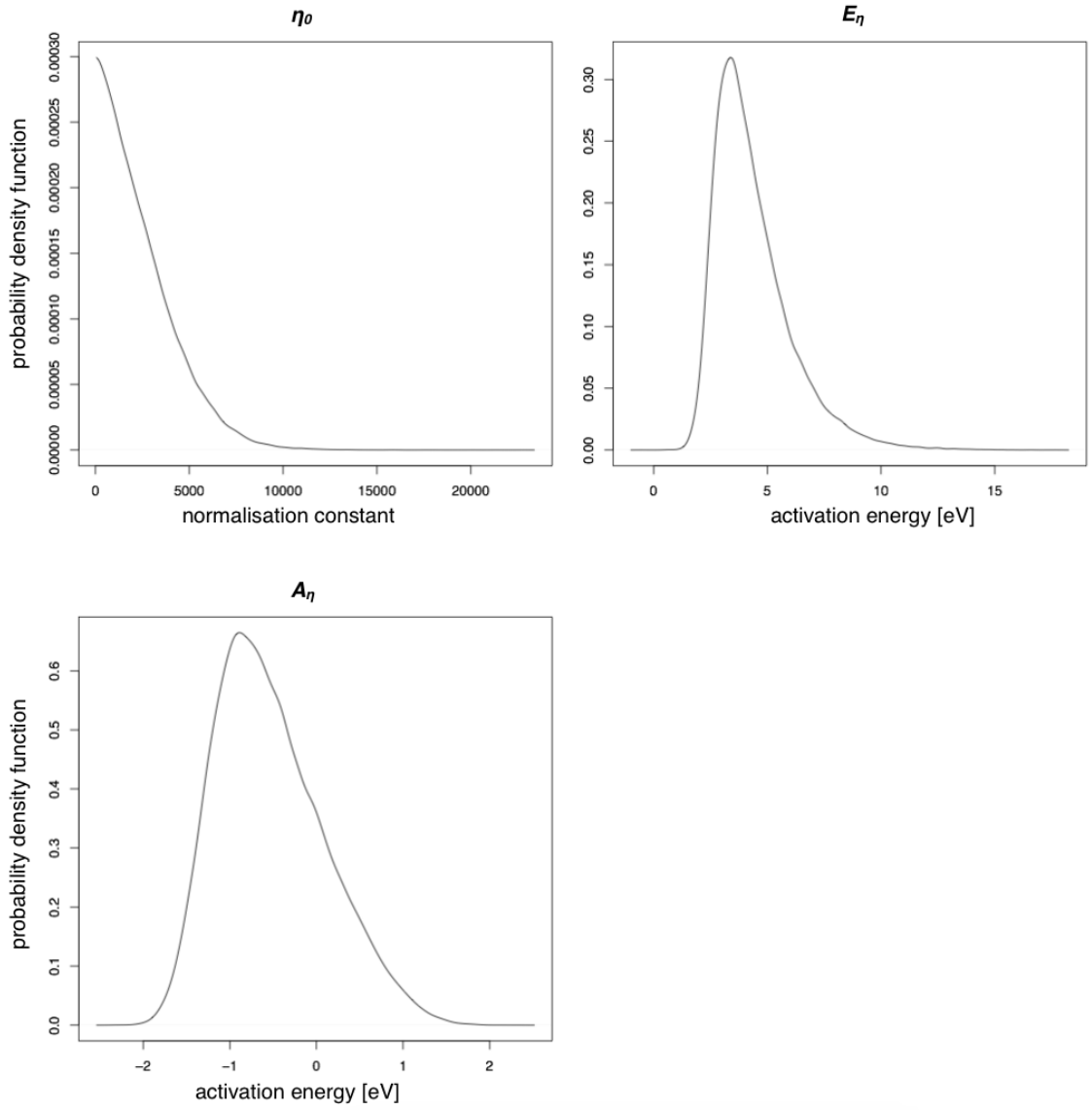

Figure 13 – **Marginal density plots** of the samples from the posterior distribution for the normalisation constant of half saturation density η_0 and, the half saturation density activation energy main effects of experimental temperature E_η and temperature adaptation A_η.

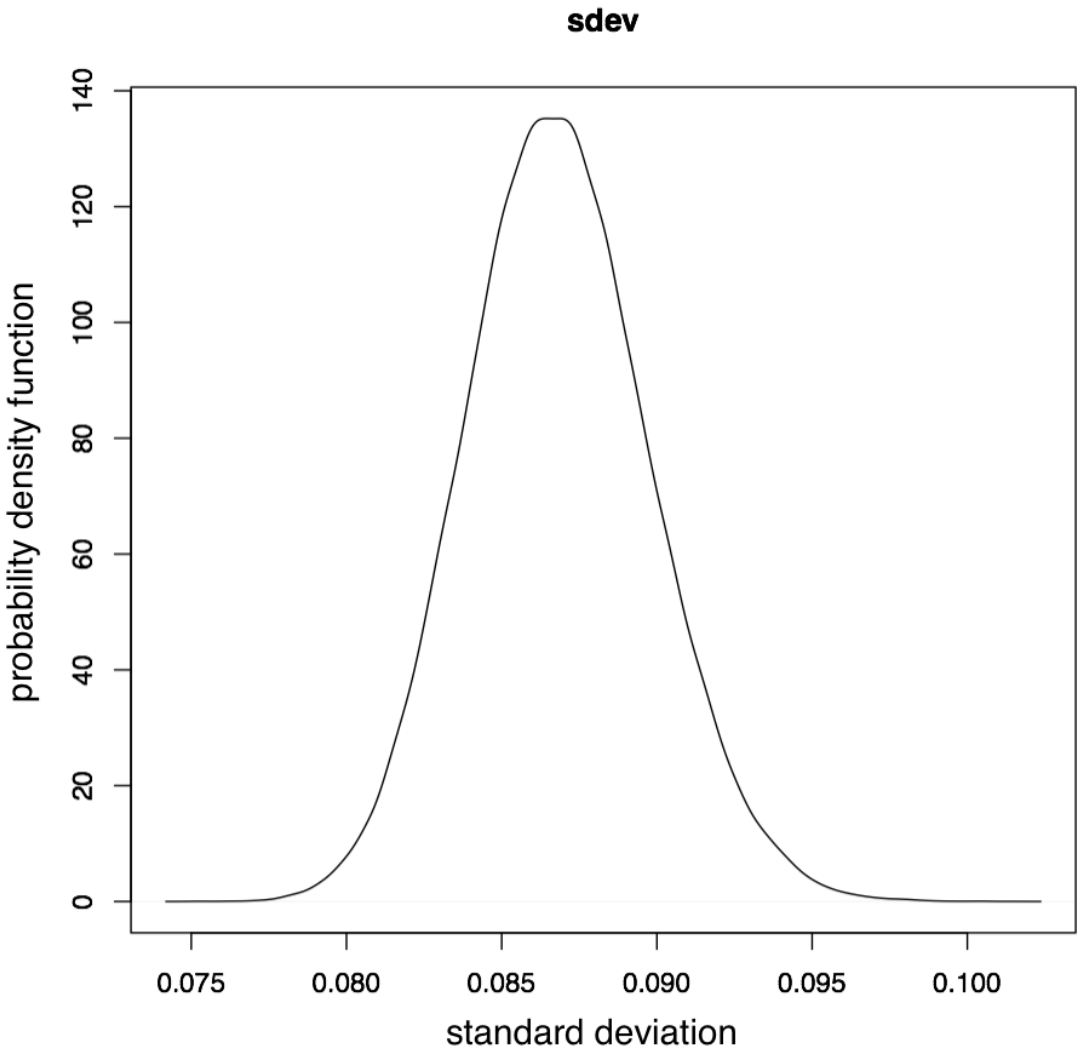

Figure 14 – **Marginal density plot** of the samples from the posterior distribution for standard deviation.

Supplementary results

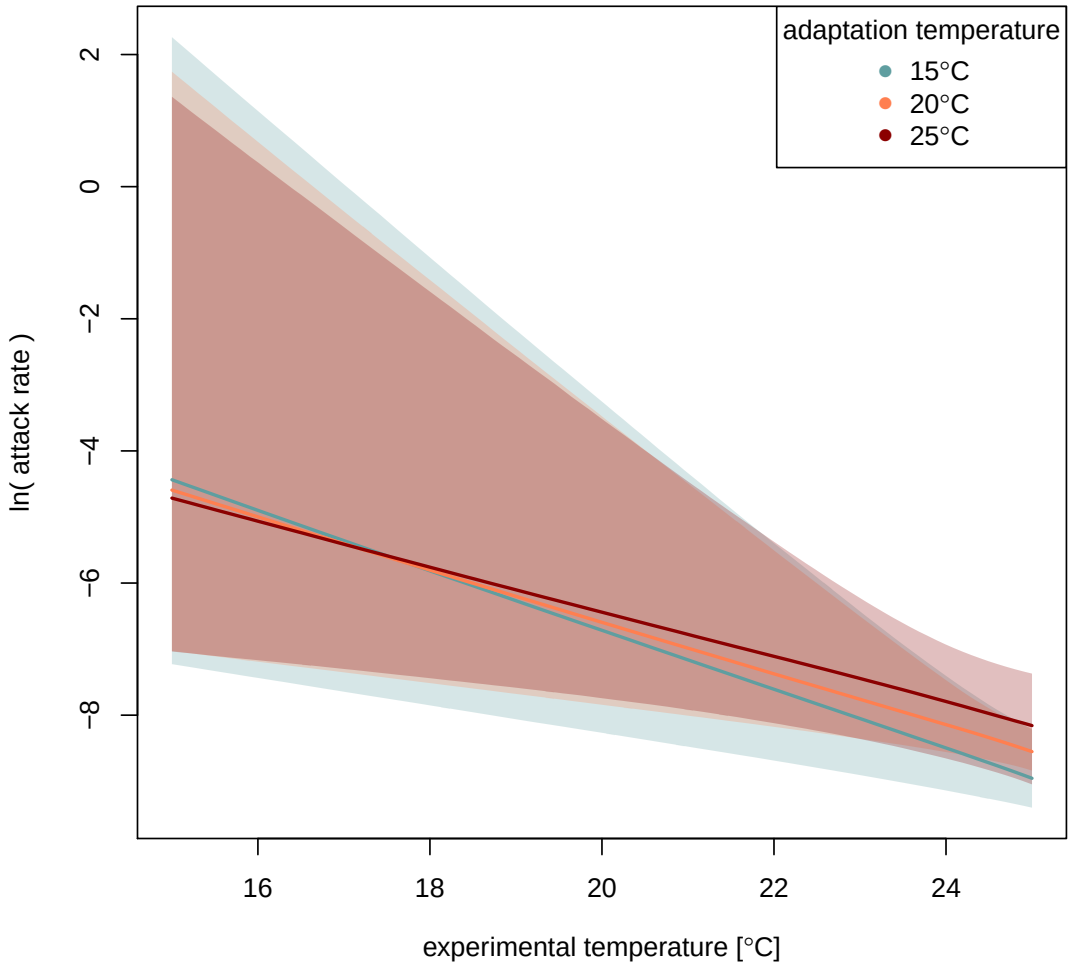

Figure 15 – **Attack rates** of *Tetrahymena pyriformis* adapted to either 15° C or 25° C preying on *Pseudomonas fluorescens* CHA19-gfp calculated from half-saturation densities and maximum feeding rates estimated by the functional response model

Table 8 – **Summary table of attack rates** a: The relation $a = f/\eta$ determines normalisation constant $a_0 = f_0/\eta_0$, activation energies for experimental temperature $E_a = E_f - E_\eta$, adaptation temperature $A_a = A_f - A_\eta$ and interactive effect $I_a = I_f$ and their distributions based on the results of model 3 (Supporting Table 7).

	mean	sd	2.5%	25%	50%	75%	97.5%
a_0	0.007	0.092	0.000	0.001	0.001	0.003	0.031
E_a	-3.305	1.692	-7.614	-4.097	-2.922	-2.108	-1.146
A_a	0.168	0.582	-1.119	-0.206	0.249	0.604	1.097
I_a	0.569	0.122	0.380	0.481	0.548	0.639	0.855

Table 9 – **Activation energies of attack rates** $\tilde{E}_a$ for predators adapted to 15° C, 20° C and 25° C for approximately 20 generations.

adaptation temperature	activation energy of attack rate $\tilde{E}_a$
15° C	-3.700
20° C	-3.305
25° C	-2.928

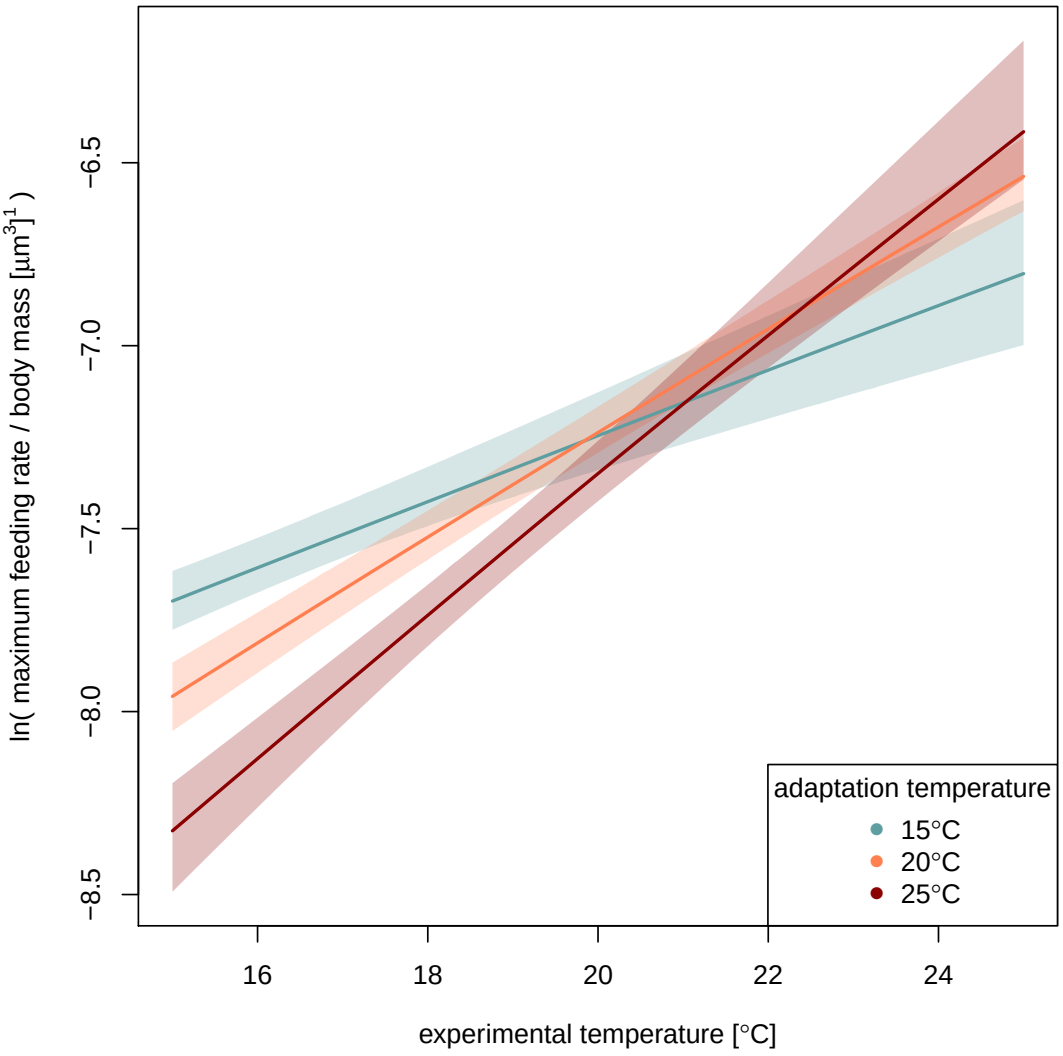

Figure 16 – **Metabolic body-mass accounted maximum feeding rates** ($f/bodymass^{1.0}[\mu m^3]$) for *Tetrahymena pyriformis* adapted to 15° C (blue), 20° C (orange) and 25° C (red) along an experimental temperature gradient. Resembling the tendencies shown for $bodymass^{0.75}[\mu m^3]$ (Figure 3.3c), predators show an increase with experimental temperature while predators adapted to 15° C and 25° C show the highest maximum feeding rates at their adapted temperature respectively. Solid lines represent median values, shaded areas indicate 95 % credibility intervals.

Model code

```
functions{
  // ODE right hand side
  // model for data with predator present
  real[] frmodelode_treatment(real t, real[] N, real[] params, real[] x_r, int[] x_i){
    real dNdt[1];
    dNdt[1] <- -( params[3]*N[1] / (params[4]+N[1]) ) * params[5] +
params[1]*N[1]*log(params[2]/N[1]);
    return dNdt;
  }
  // model for control data (equivalent to treatment model for Pstart=params[5]=0, but
more efficient)
  real[] frmodelode_control(real t, real[] N, real[] params, real[] x_r, int[] x_i){
    real dNdt[1];
    dNdt[1] <- params[1]*N[1]*log(params[2]/N[1]);
    return dNdt;
  }
}

data{
  int M;                // Sample size
  real logNend[M];      // log of final density
  real tempArrExp[M];   // Arrhenius temperature experiment
  real tempArrAdapt[M]; // Arrhenius temperature adaption
  real Nstart[M];       // initial density
  real Tend[M,2];       // Tend[,2]: duration time of measurement, Tend[,1]: dummy used
for the stan function integrate_ode()
  real Pstart[M];       // predator density (0 or 100 in our data)
}

transformed data { // for the stan function integrate_ode(), not used here
  real x_r[0];
  int x_i[0];
}

parameters {  // see manuscript for parameter definition
  real<lower=0> r;
  real<lower=0> K;
  real E_r;
  real E_K;
  real<lower=0> Fmax;
  real<lower=0> Nhalf;
  real E_Fmax;
  real E_Nhalf;
  real A_Fmax;
  real A_Nhalf;
  real I_Fmax;
  real<lower=0> sdev;
}

model {
  // intermediate parameters for handling the stan function integrate_ode()
  real params[5]; // input parameters for ODE
  real N0[1];     // initial value, needs to be a vector for stan. dim = #(equations in
ODE)
  real Nend[2,1]; // output values, needs to be a matrix for stan. dim1 = #(outputs),
dim2 = #(equations in ODE)

  // priors (uninformative)
  r ~ normal(0, 100);
  K ~ normal(0, 100000);
  E_r ~ normal(0, 100);
  E_K ~ normal(0, 100);
  Fmax ~ normal(0, 100);
  Nhalf ~ normal(0, 100000);
  E_Fmax ~ normal(0, 100);
  E_Nhalf ~ normal(0, 100);
  A_Fmax ~ normal(0, 100);
  A_Nhalf ~ normal(0, 100);
  I_Fmax ~ normal(0, 100);
  sdev ~ uniform(0, 100);

  // likelihood
  for (i in 1:M){
    params[1] <- r * exp(E_r * tempArrExp[i]); // growth rate
    params[2] <- K * exp(E_K * tempArrExp[i]); // carrying capacity
```

```
    params[3] <- Fmax * exp(E_Fmax*tempArrExp[i] + A_Fmax*tempArrAdapt[i] +
I_Fmax*tempArrExp[i]*tempArrAdapt[i]); // maximum feeding rate
    params[4] <- Nhalf * exp(E_Nhalf*tempArrExp[i] + A_Nhalf*tempArrAdapt[i]); // half
saturation density
    params[5] <- Pstart[i]; // predator density

    // compute abundance in t=Tend by numerical simulation
    N0[1] <- Nstart[i]; // hand over scalar initial abundance to vector
    if (params[5]>0) { // predator present
      Nend <- integrate_ode(frmodelode_treatment,N0,0,Tend[i],params,x_r,x_i);
    }
    else { // control data
      Nend <- integrate_ode(frmodelode_control,N0,0,Tend[i],params,x_r,x_i);
    }
    // connect model result to data logNend for likelihood
    logNend[i] ~ normal(log(Nend[2,1]),sdev);
  }
}

generated quantities { // for model comparison only. repeat the steps of the model block
and save log-likelihood value, see loo package
  real params[5];
  real N0[1];
  real Nend[2,1];
  vector[M] log_lik; // log likelihood values for all observations

  for (i in 1:M){
    params[1] <- r * exp(E_r * tempArrExp[i]);
    params[2] <- K * exp(E_K * tempArrExp[i]);
    params[3] <- Fmax * exp(E_Fmax*tempArrExp[i] + A_Fmax*tempArrAdapt[i] +
I_Fmax*tempArrExp[i]*tempArrAdapt[i]);
    params[4] <- Nhalf * exp(E_Nhalf*tempArrExp[i] + A_Nhalf*tempArrAdapt[i]);
    params[5] <- Pstart[i];

    N0[1] <- Nstart[i];
    if (params[5]>0) {
      Nend <- integrate_ode(frmodelode_treatment,N0,0,Tend[i],params,x_r,x_i);
    }
    else {
      Nend <- integrate_ode(frmodelode_control,N0,0,Tend[i],params,x_r,x_i);
    }

    // compute normal_log value for log-likelhood of lognormal distribution
    log_lik[i] <- normal_log(logNend[i], log(Nend[2,1]), sdev);
  }
}
```

Temperature adaptation of predator interference

Methods

Table 10 – Number of experimental treatments run at 15° C, 20° C and 25° C experimental temperatures for control treatments containing only bacterial prey but no predators, and functional response treatments for predators adapted to 15° C, 20° C and 25° C adaptation temperature for approximately 20 generations. Overall we measured 731 control treatments and 1353 functional response treatments.

adaptation temperature	experimental temperature 15° C	experimental temperature 20° C	experimental temperature 25° C
control	243	249	239
15° C	229	180	159
20° C	153	121	94
25° C	158	135	124

Model analysis

Table 11 – Summary statistics of the control treatments: Summary table of the samples from the posterior distribution showing the mean values, standard deviations and quantiles of the normalisation constants of growth rate r_0 and carrying capacity K_0 and their activation energies E_r and E_K for the prey *Pseudomonas fluorescens* CHA19-gfp in treatments without predators.

	mean	se_{mean}	sd	2.5 %	25 %	50 %	75 %	97.5 %	n_{eff}	Rhat
$ln(r_0)$	-8.049	0.001	0.044	-8.139	-8.077	-8.047	-8.019	-7.965	4184	1.000
E_r	0.705	0.001	0.077	0.558	0.653	0.703	0.755	0.860	4282	1.000
$ln(K_0)$	12.479	0.001	0.051	12.382	12.444	12.477	12.512	12.582	4023	1.001
E_K	-0.285	0.001	0.090	-0.468	-0.345	-0.282	-0.223	-0.114	3910	1.002
$sdev$	0.109	0.000	0.001	0.107	0.108	0.109	0.110	0.112	5356	1.000

Table 12 – Summary statistics of the Holling type 2 ordinary differential equation model: Summary table of the samples from the posterior distribution showing the mean values, standard deviations and quantiles of the normalisation constants of the attack rate a_0 and handling time h_0 and their activation energy main effects of experimental temperature E_a, E_h, of adaptive temperature A_a, A_h, and the interaction terms I_a, I_h.

	mean	se_{mean}	sd	2.5 %	25 %	50 %	75 %	97.5 %	n_{eff}	Rhat
$ln(a_0)$	-11.165	0.002	0.098	-11.359	-11.230	-11.165	-11.100	-10.976	3379	1.001
E_a	-2.558	0.004	0.222	-3.010	-2.700	-2.552	-2.406	-2.140	3610	1.002
A_a	1.1588	0.003	0.151	0.863	1.056	1.159	1.260	1.452	3552	1.001
I_a	-2.741	0.005	0.329	-3.417	-2.957	-2.733	-2.519	-2.120	3665	1.002
$ln(h_0)$	-1.372	0.003	0.166	-1.719	-1.478	-1.366	-1.258	-1.064	3651	1.001
E_h	-4.642	0.005	0.314	-5.304	-4.847	-4.624	-4.426	-4.063	4479	1.000
A_h	5.898	0.007	0.466	5.068	5.567	5.876	6.194	6.870	4531	1.001
I_h	0.948	0.012	0.793	-0.587	0.412	0.933	1.470	2.545	4732	1.001
$sdev$	0.292	0.000	0.003	0.286	0.290	0.292	0.294	0.297	8065	1.000

Table 13 – Summary statistics of the Holling type 3 ordinary differential equation model: Summary table of the samples from the posterior distribution showing the mean values, standard deviations and quantiles of the normalisation constants of the attack coefficient b_0 and handling time h_0 and their activation energy main effects of experimental temperature E_b, E_h, of adaptive temperature A_b, A_h, and the interaction terms I_b, I_h.

	mean	se_{mean}	sd	2.5 %	25 %	50 %	75 %	97.5 %	n_{eff}	Rhat
$ln(b_0)$	-23.515	0.001	0.075	-23.663	-23.566	-23.515	-23.465	-23.370	7793	1.000
E_b	-0.671	0.002	0.143	-0.947	-0.767	-0.672	-0.574	-0.381	6031	1.000
A_b	-0.620	0.002	0.145	-0.919	-0.714	-0.617	-0.524	-0.346	4743	1.001
I_b	0.428	0.004	0.262	-0.097	0.256	0.433	0.602	0.936	4504	1.001
$ln(h_0)$	-0.437	0.001	0.070	-0.575	-0.483	-0.436	-0.390	-0.302	6757	1.000
E_h	-0.266	0.002	0.133	-0.530	-0.356	-0.266	-0.178	-0.002	6248	1.000
A_h	0.774	0.003	0.167	0.433	0.664	0.780	0.885	1.090	4146	1.001
I_h	-0.318	0.005	0.290	-0.904	-0.504	-0.303	-0.123	0.227	3843	1.001
$sdev$	0.291	0.000	0.003	0.286	0.289	0.291	0.293	0.297	10000	1.000

Table 14 – Summary statistics of the Beddington-DeAngelis type 2 ordinary differential equation model: Summary table of the samples from the posterior distribution showing the mean values, standard deviations and quantiles of the normalisation constants of the attack rate a_0, handling time h_0 and the interference coefficient c_0 and their activation energy main effects of experimental temperature E_a, E_h, E_c, of adaptive temperature A_a, A_h, A_c, and the interaction terms I_a, I_h, I_c.

	mean	se_{mean}	sd	2.5 %	25 %	50 %	75 %	97.5 %	n_{eff}	Rhat
$ln(a_0)$	-8.707	0.002	0.121	-8.927	-8.792	-8.711	-8.629	-8.452	2380	1.002
E_a	1.356	0.005	0.238	0.862	1.200	1.370	1.521	1.791	2317	1.002
A_a	0.414	0.004	0.197	0.048	0.277	0.408	0.543	0.821	2230	1.001
I_a	0.081	0.008	0.373	-0.726	-0.157	0.103	0.339	0.751	2241	1.002
$ln(h_0)$	-1.931	0.001	0.047	-2.031	-1.962	-1.929	-1.899	-1.844	2588	1.001
E_h	-0.860	0.002	0.083	-1.025	-0.916	-0.858	-0.804	-0.699	2493	1.001
A_h	0.708	0.002	0.084	0.533	0.654	0.712	0.767	0.859	2442	1.001
I_h	-0.363	0.003	0.146	-0.647	-0.462	-0.366	-0.268	-0.067	2425	1.001
$ln(c_0)$	-2.187	0.002	0.118	-2.403	-2.269	-2.191	-2.113	-1.937	2459	1.002
E_c	1.584	0.005	0.236	1.096	1.429	1.595	1.745	2.018	2384	1.002
A_c	1.066	0.004	0.195	0.705	0.930	1.059	1.196	1.470	2345	1.001
I_c	-0.332	0.008	0.373	-1.127	-0.571	-0.310	-0.075	0.344	2337	1.002
sdev	0.203	0.000	0.002	0.199	0.201	0.203	0.204	0.206	7122	1.000

Table 15 – Summary statistics of the Beddington-DeAngelis type 3 ordinary differential equation model: Summary table of the samples from the posterior distribution showing the mean values, standard deviations and quantiles of the normalisation constants of the attack rate b_0, handling time h_0 and the interference coefficient c_0 and their activation energy main effects of experimental temperature E_b, E_h, E_c, of adaptive temperature A_b, A_h, A_c, and the interaction terms I_b, I_h, I_c.

	mean	se_{mean}	sd	2.5 %	25 %	50 %	75 %	97.5 %	n_{eff}	Rhat
$ln(b_0)$	-18.473	0.003	0.154	-18.840	-18.566	-18.444	-18.354	-18.257	2632	1.001
E_b	0.174	0.012	0.562	-0.842	-0.226	0.1463	0.569	1.292	2342	1.003
A_b	0.903	0.005	0.285	0.296	0.719	0.923	1.104	1.403	2862	1.001
I_b	-0.083	0.018	0.860	-1.684	-0.691	-0.110	0.507	1.610	2343	1.003
$ln(h_0)$	-1.432	0.000	0.023	-1.477	-1.447	-1.432	-1.417	-1.386	5851	1.000
E_h	-1.308	0.001	0.045	-1.395	-1.337	-1.307	-1.278	-1.221	4248	1.001
A_h	0.606	0.001	0.037	0.532	0.581	0.606	0.631	0.680	5388	1.000
I_h	-0.278	0.001	0.070	-0.416	-0.326	-0.278	-0.229	-0.144	4630	1.001
$ln(c_0)$	-0.197	0.003	0.149	-0.550	-0.288	-0.166	-0.079	-0.008	2627	1.001
E_c	1.225	0.011	0.552	0.222	0.831	1.196	1.613	2.327	2371	1.003
A_c	1.496	0.005	0.280	0.899	1.318	1.514	1.696	1.990	2916	1.001
I_c	-0.358	0.017	0.849	-1.941	-0.959	-0.381	0.225	1.320	2375	1.003
$sdev$	0.219	0.000	0.002	0.215	0.217	0.219	0.220	0.223	9281	1.000

Table 16 – Summary statistics of the Crowley-Martin type 2 ordinary differential equation model: Summary table of the samples from the posterior distribution showing the mean values, standard deviations and quantiles of the normalisation constants of the attack rate a_0, handling time h_0 and the interference coefficient c_0 and their activation energy main effects of experimental temperature E_a, E_h, E_c, of adaptive temperature A_a, A_h, A_c, and the interaction terms I_a, I_h, I_c.

	mean	se_{mean}	sd	2.5 %	25 %	50 %	75 %	97.5 %	n_{eff}	Rhat
$ln(a_0)$	-9.55	0.000	0.036	-9.620	-9.574	-9.550	-9.527	-9.480	6812	1.000
E_a	1.258	0.001	0.079	1.103	1.203	1.257	1.310	1.417	4936	1.000
A_a	-0.392	0.001	0.064	-0.519	-0.435	-0.391	-0.348	-0.265	5931	1.000
I_a	-0.436	0.002	0.127	-0.677	-0.523	-0.438	-0.350	-0.185	5011	1.001
$ln(h_0)$	-2.664	0.001	0.050	-2.768	-2.696	-2.662	-2.629	-2.571	5031	1.001
E_h	-0.350	0.001	0.100	-0.537	-0.417	-0.354	-0.286	-0.141	4560	1.000
A_h	0.271	0.001	0.093	0.078	0.212	0.274	0.333	0.444	4780	1.000
I_h	-0.424	0.003	0.172	-0.749	-0.541	-0.429	-0.316	-0.067	4480	1.001
$ln(c_0)$	-3.545	0.000	0.030	-3.605	-3.565	-3.544	-3.524	-3.486	6810	1.001
E_c	1.091	0.001	0.058	0.978	1.052	1.091	1.130	1.205	6385	1.000
A_c	0.423	0.001	0.049	0.326	0.391	0.424	0.457	0.519	6786	1.000
I_c	-0.561	0.001	0.094	-0.742	-0.624	-0.561	-0.498	-0.373	6369	1.000
sdev	0.204	0.000	0.002	0.200	0.202	0.204	0.205	0.207	10000	1.000

Table 17 – Summary statistics of the Crowley-Martin type 3 ordinary differential equation model: Summary table of the samples from the posterior distribution showing the mean values, standard deviations and quantiles of the normalisation constants of the attack coefficient b_0, handling time h_0 and the interference coefficient c_0 and their activation energy main effects of experimental temperature E_b, E_h, E_c, of adaptive temperature A_b, A_h, A_c, and the interaction terms I_b, I_h, I_c.

	mean	se_{mean}	sd	2.5 %	25 %	50 %	75 %	97.5 %	n_{eff}	Rhat
$ln(b_0)$	-20.487	0.000	0.041	-20.569	-20.514	-20.487	-20.459	-20.405	10000	1.000
E_b	0.960	0.001	0.081	0.802	0.906	0.959	1.014	1.119	7720	1.000
A_b	-0.414	0.001	0.071	-0.553	-0.463	-0.415	-0.367	-0.277	7994	1.001
I_b	-0.590	0.002	0.134	-0.853	-0.680	-0.592	-0.500	-0.329	7884	1.000
$ln(h_0)$	-2.138	0.000	0.024	-2.185	-2.154	-2.138	-2.123	-2.092	5854	1.000
E_h	-0.761	0.001	0.043	-0.846	-0.790	-0.761	-0.732	-0.678	5471	1.001
A_h	0.267	0.001	0.038	0.192	0.242	0.268	0.293	0.345	5661	1.000
I_h	-0.161	0.001	0.070	-0.297	-0.208	-0.161	-0.115	-0.023	5989	1.001
$ln(c_0)$	-3.616	0.000	0.029	-3.672	-3.634	-3.615	-3.595	-3.558	6420	1.001
E_c	1.001	0.001	0.054	0.895	0.965	1.000	1.037	1.111	5089	1.001
A_c	0.346	0.001	0.048	0.253	0.314	0.347	0.379	0.439	5658	1.001
I_c	-0.615	0.001	0.088	-0.788	-0.674	-0.616	-0.557	-0.441	5712	1.001
$sdev$	0.197	0.000	0.002	0.194	0.196	0.197	0.199	0.201	10000	1.000

Density distributions

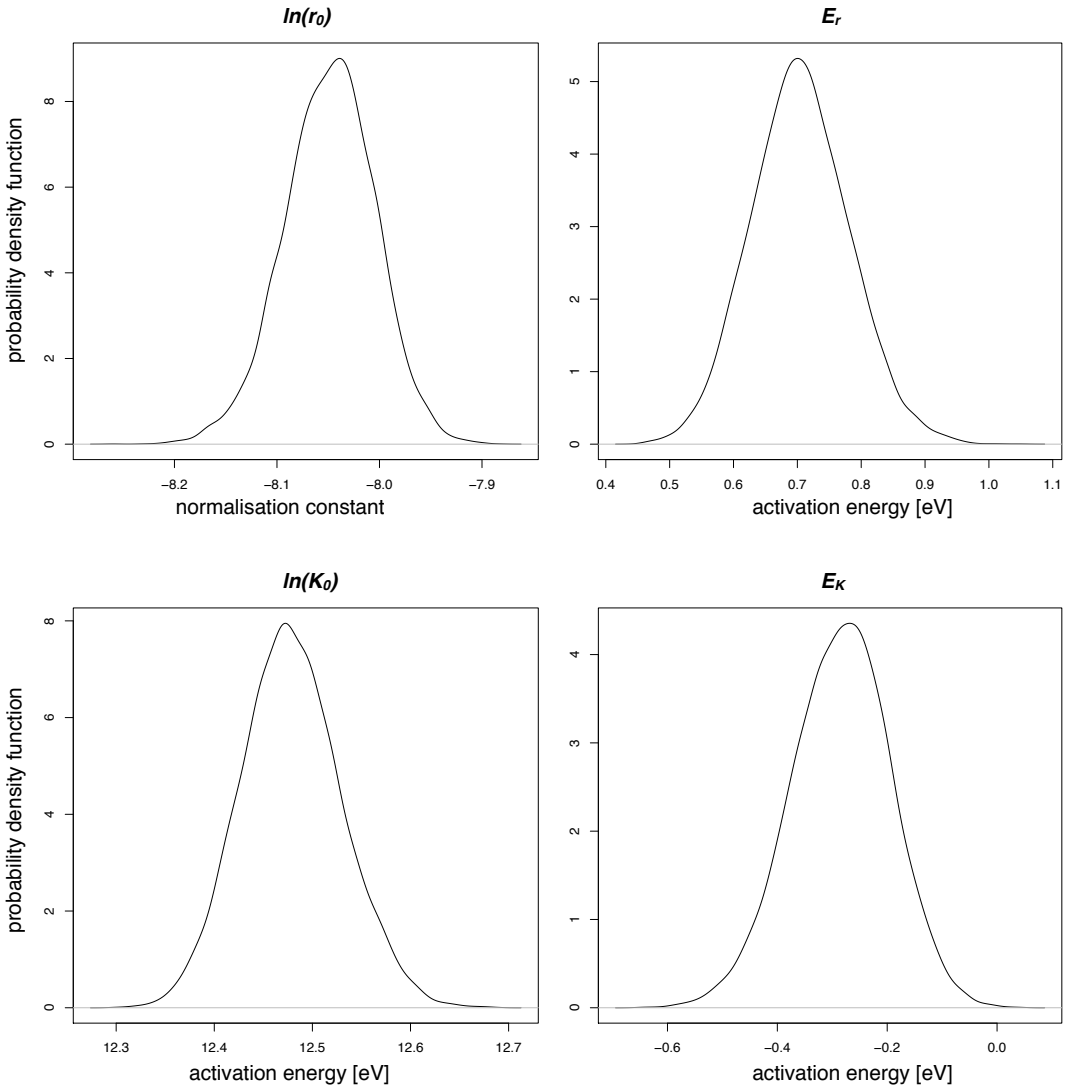

Figure 17 – **Marginal density plots** of the samples from the posterior distribution for maximum growth rate r and carrying capacity K) parameters for the bacterial prey *Pseudomonas fluorescens* CHA19-gfp in control treatments.

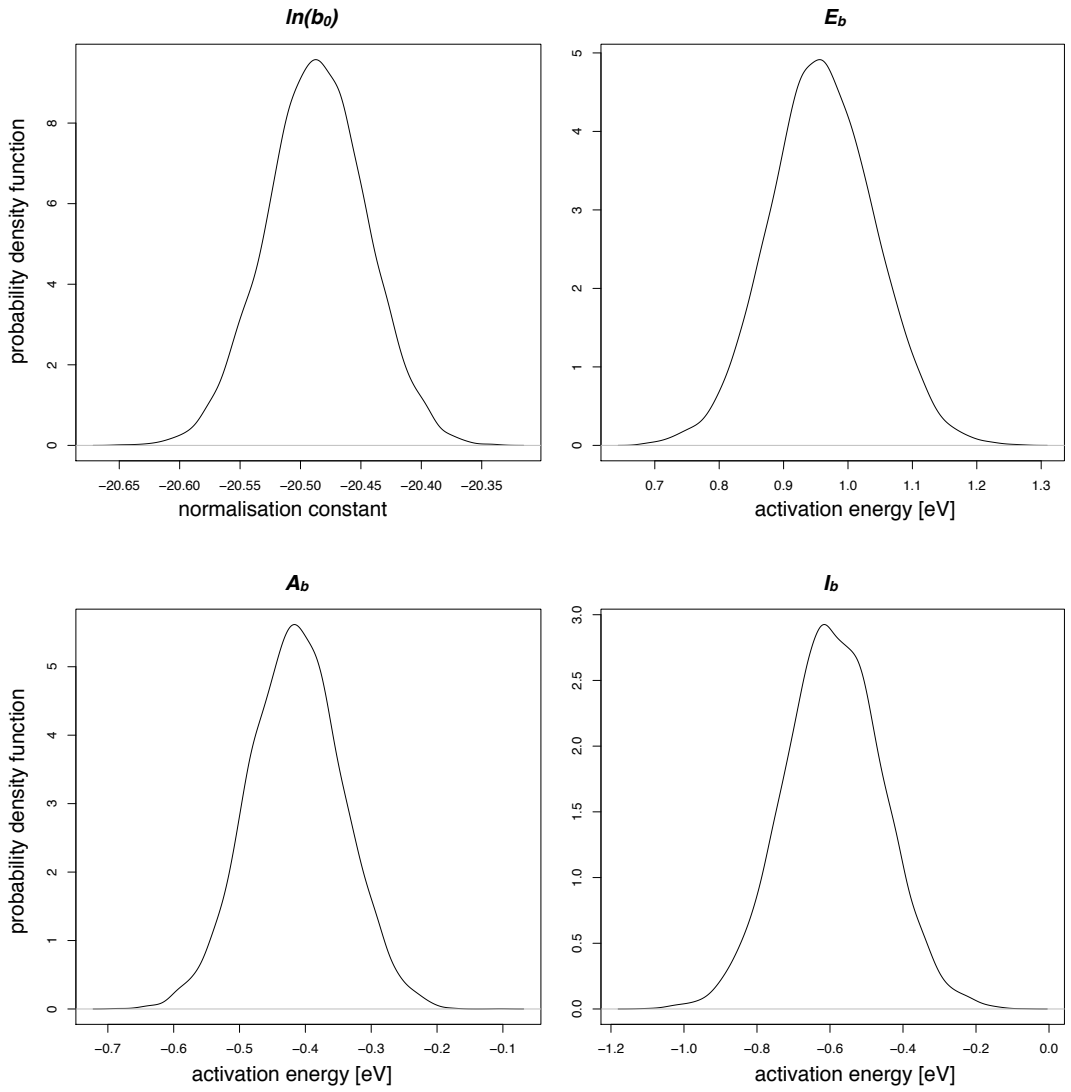

Figure 18 – **Marginal density plots** of the samples from the posterior distribution for the normalisation constant of attack rate $ln(b_0)$ and, the activation energy main effects of experimental temperature E_b, temperature adaptation A_b and interaction effect I_b.

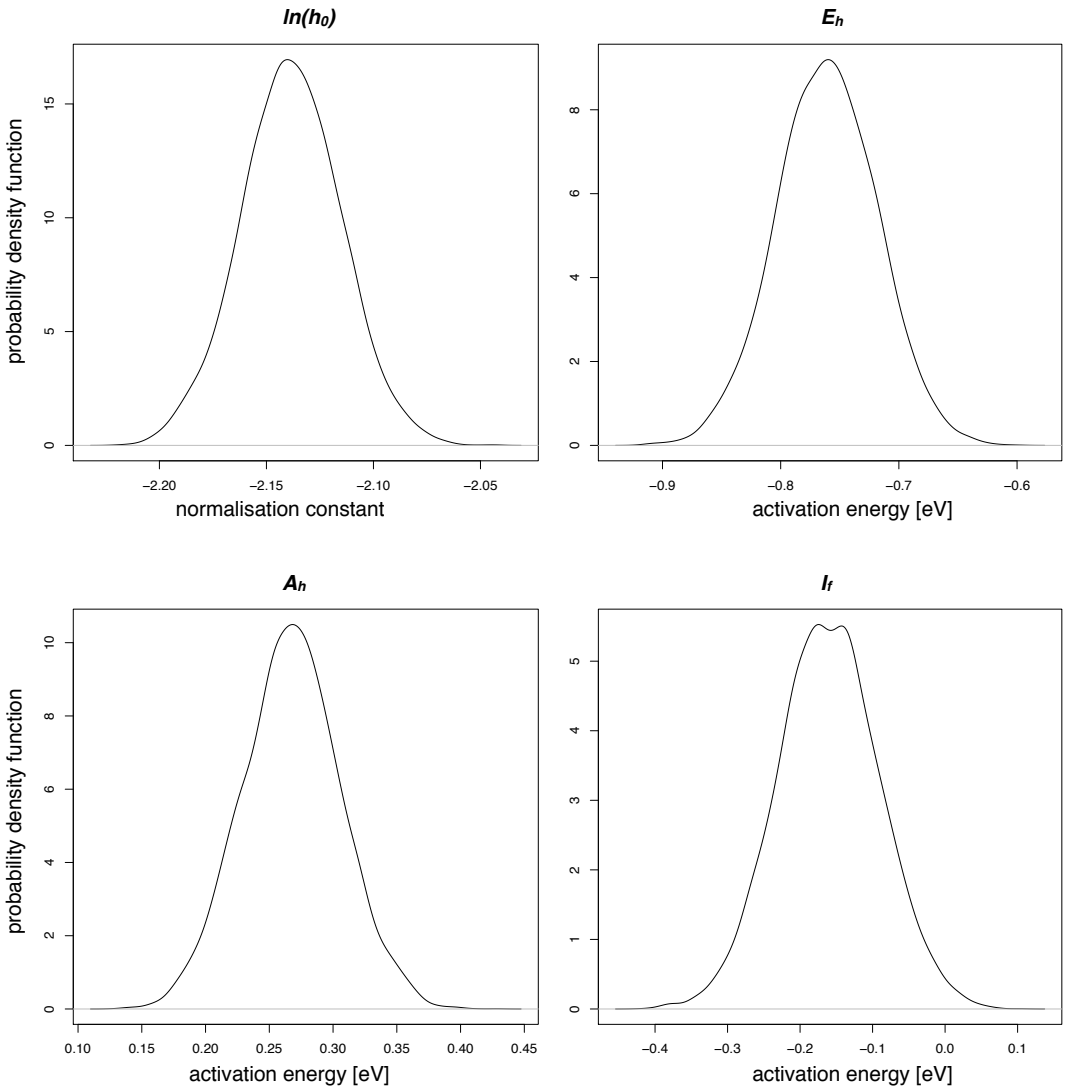

Figure 19 – **Marginal density plots** of the samples from the posterior distribution for the normalisation constant of handling time $ln(h_0)$ and, the activation energy main effects of experimental temperature E_h, temperature adaptation A_h and interaction effect I_h.

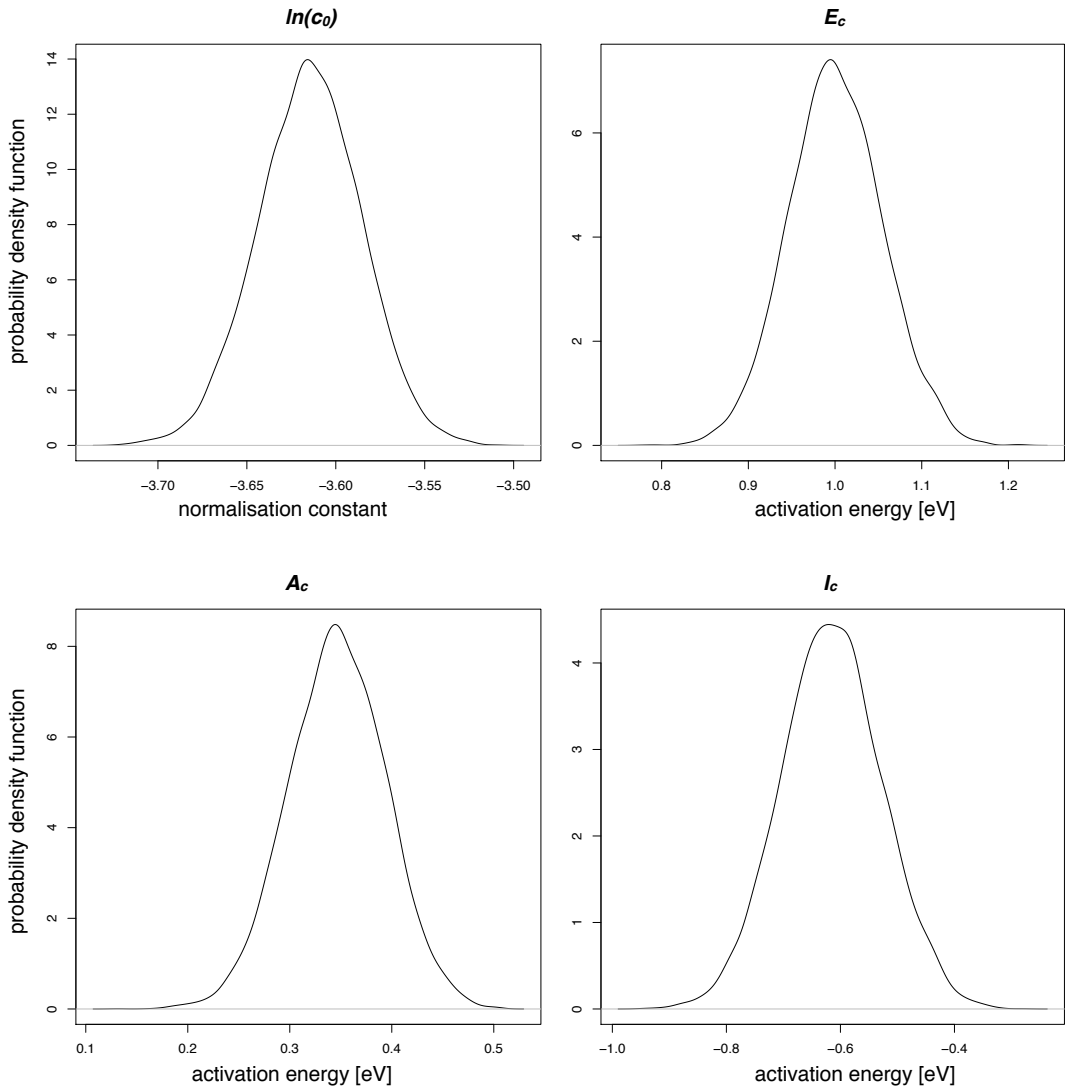

Figure 20 – **Marginal density plots** of the samples from the posterior distribution for the normalisation constant of interference $ln(c_0)$ and, the activation energy main effects of experimental temperature E_c, temperature adaptation A_c and interaction effect I_c.

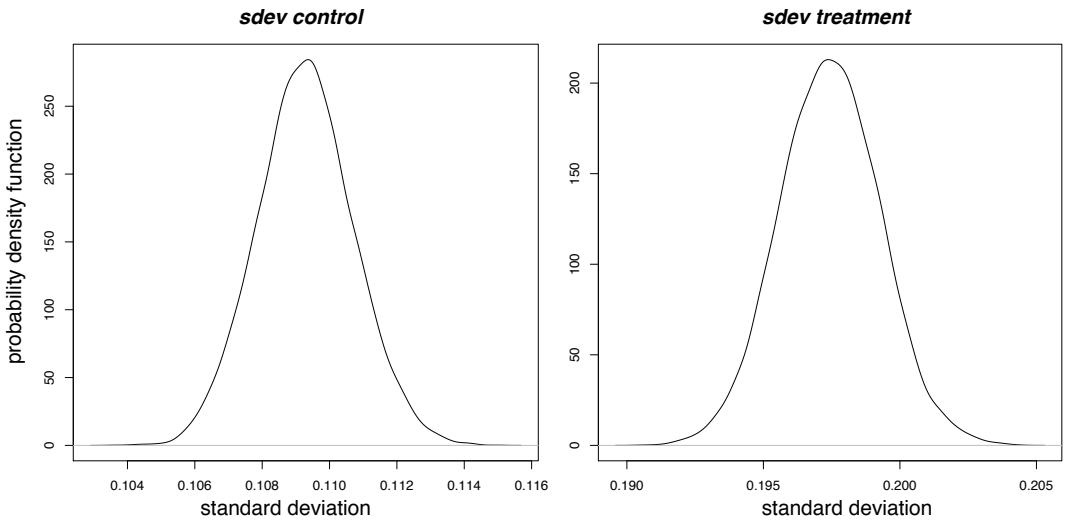

Figure 21 – **Marginal density plot** of the samples from the posterior distribution for standard deviation of control treatments and experimental functional response treatments.

Supplementary results

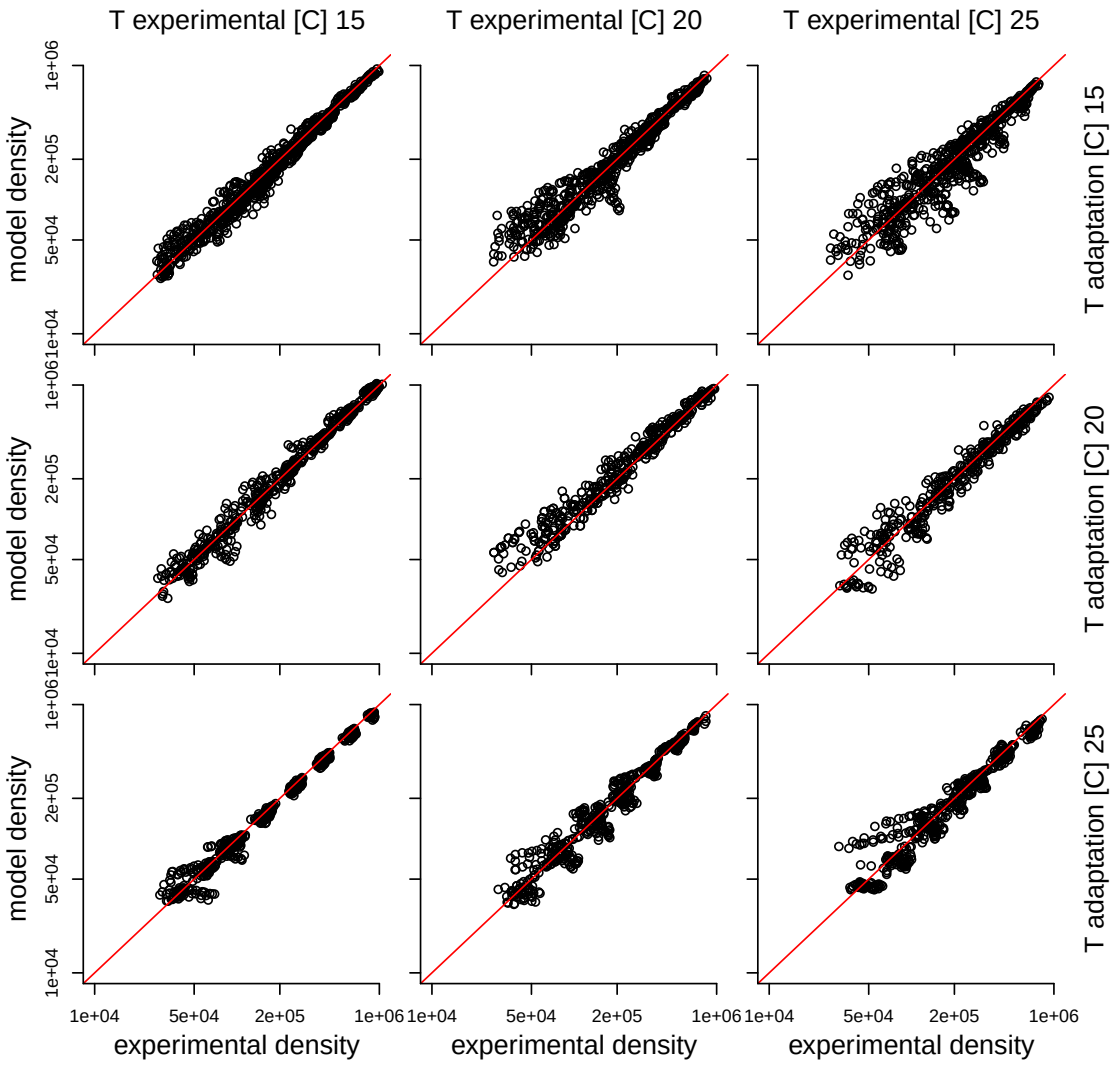

Figure 22 – Measured experimental densities in prey μl^{-1} plotted against prey densities in prey μl^{-1} predicted by the Crowley-Martin Type 3 ordinary differential equation model, for predators adapted to 15°C, 20°C and 25°C at the experimental temperatures of 15°C, 20°C and 25°C. Red lines mark the optimal relationship.

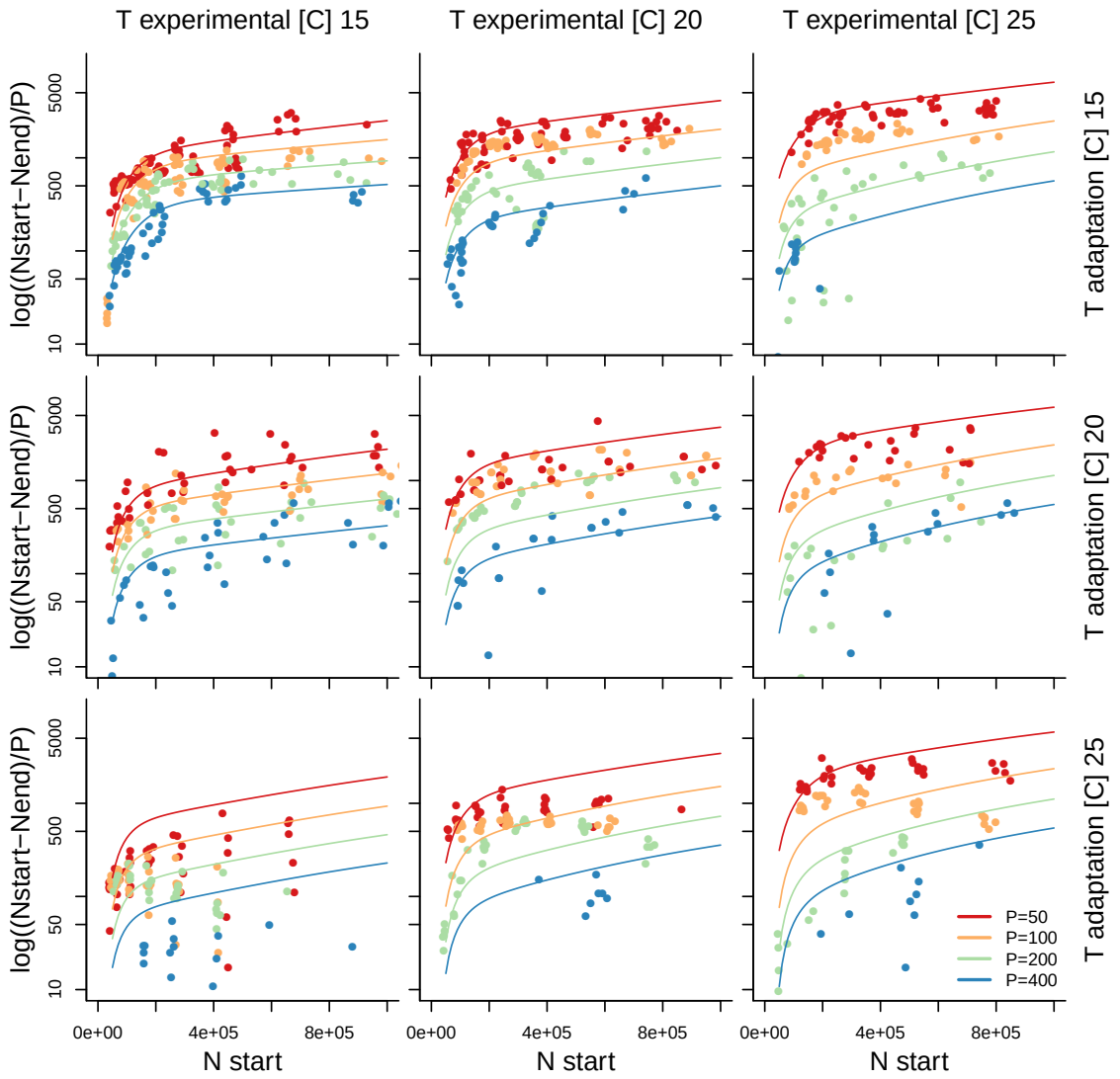

Figure 23 – **Crowley-Martin type 3 ordinary differential equation model** (equation 5b) fitted through data with initial prey density plotted against final prey densities for predators adapted to 15° C, 20° C and 25° C at 15° C, 20° C and 25° C experimental temperature. Please note, that due to the Gompertz growth term in the ODE, final prey densities not only concern eaten prey organisms but also account for natural prey growth and death during the experiment and all values are calculated per-capita predator (densities in predators μl^{-1}).

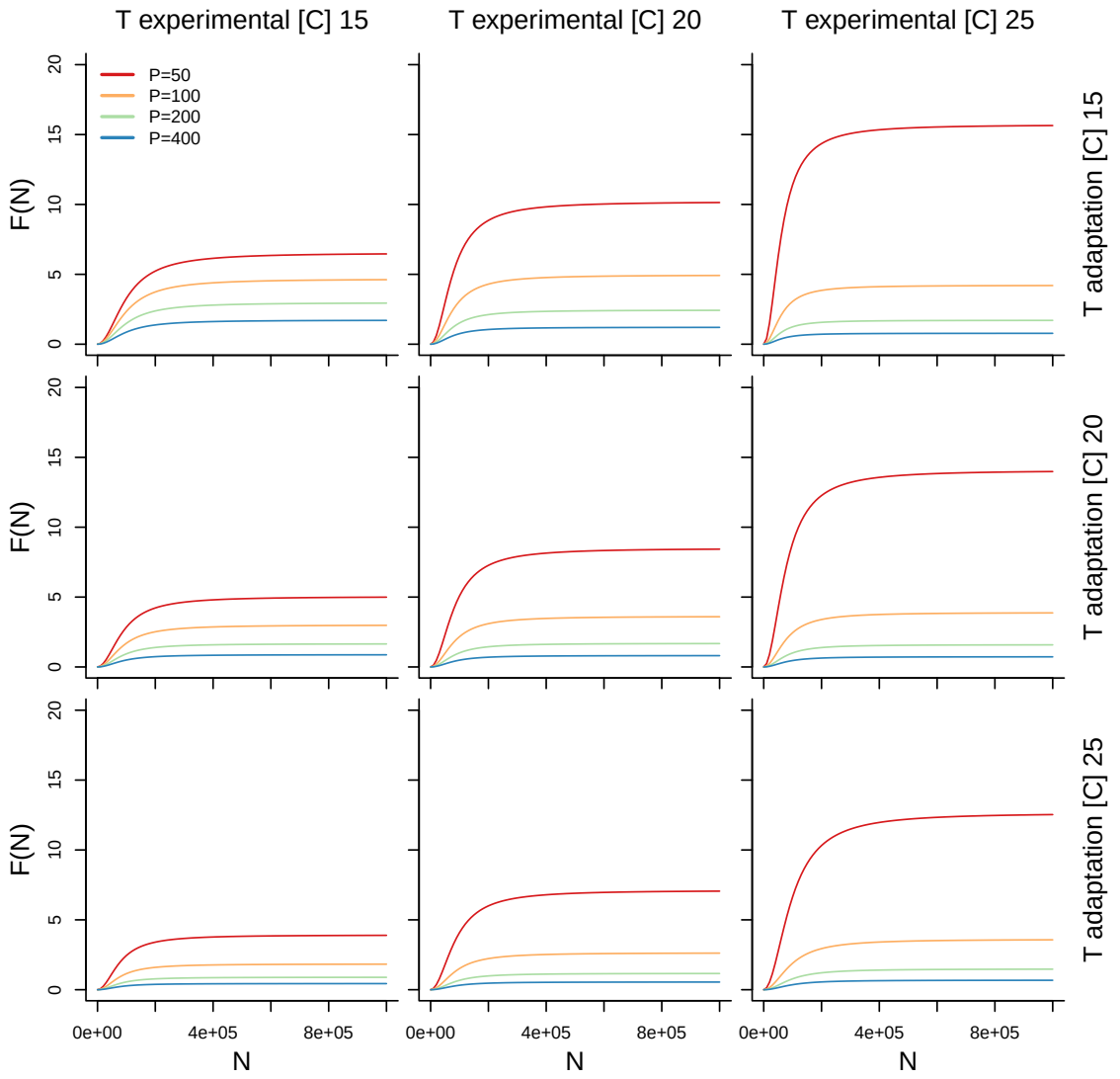

Figure 24 – **Crowley-Martin type 3 functional response** at 15° C, 20° C and 25° C experimental temperature for predators adapted to 15° C, 20° C and 25° C, predator densities are given in predators μl^{-1}.

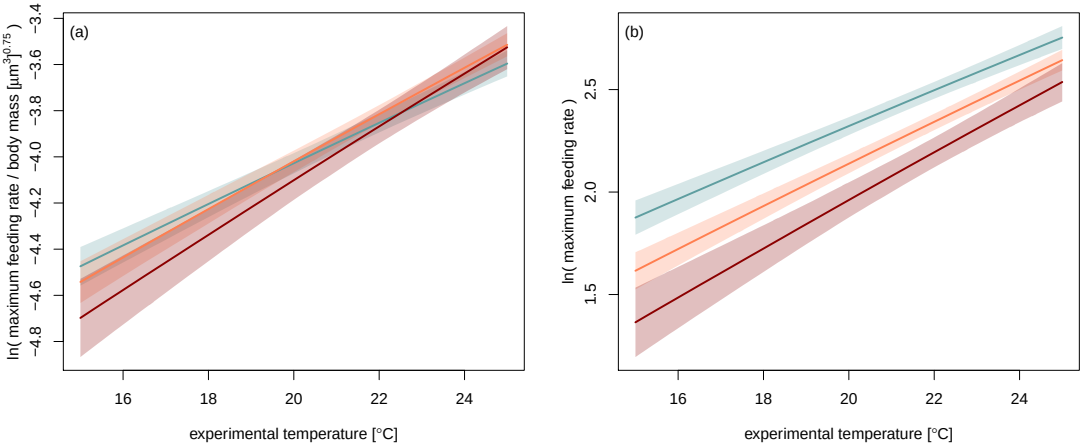

Figure 25 – **Maximum feeding rates** at 15° C, 20° C and 25° C experimental temperature for *Tetrahymena pyriformis* adapted to 15° C or 25° C preying on *Pseudomonas fluorescens* CHA19-gfp calculated from handling times estimated by the Crowley-Martin type 3 ordinary differential equation model. **a** Metabolic body-mass accounted maximum feeding rates ($f/bodymass^{1.0}[\mu m^3]$) generally increase with experimental temperature, with the steepest increase for predators adapted to 25° C. At 25° C experimental temperature, all predators show similar maximum feeding rates. **b** realised maximum feeding rates generally increase with increasing experimental temperature, predators adapted to 15°C show a shallower increase but generally higher maximum feeding rates than predators adapted to 25° C.

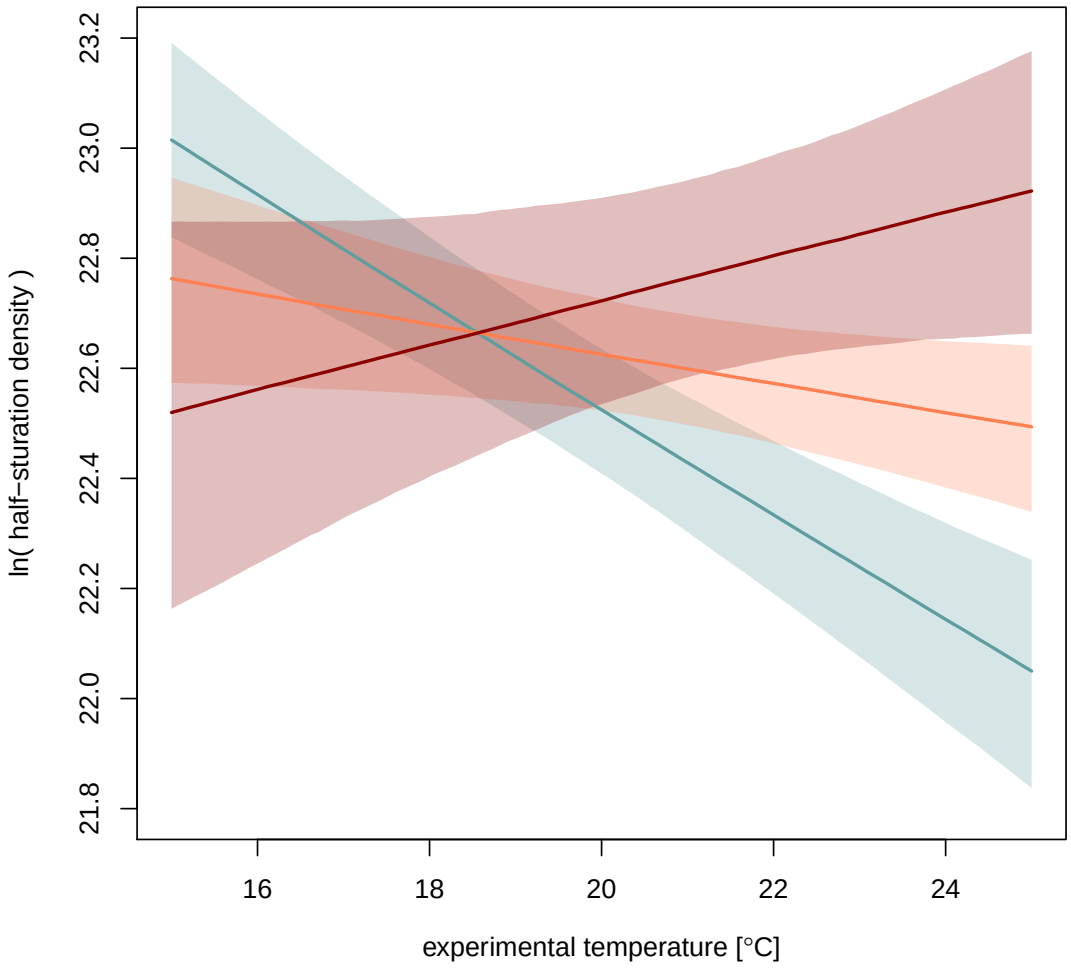

Figure 26 – **Half-saturation densities** at 15° C, 20° C and 25° C experimental temperature for *Tetrahymena pyriformis* adapted to 15° C or 25° C preying on *Pseudomonas fluorescens* CHA19-gfp calculated from handling times and attack rates ($\eta = f/a = 1/(ha)$) estimated by the Crowley-Martin type 3 ordinary differential equation model.

```
// Stan model code for control treatments: "Temperature adaptation of predator interference"; K.E. Fussmann, B. Rosenbaum, B.C. Rall; 2016

functions{
// ODE right hand side for control, only growth model
  real[] frmodelode(real t, real[] N, real[] p, real[] x_r, int[] x_i){
    real dNdt[1];
    dNdt[1] <- p[1]*N[1]*log(p[2]/N[1]);
    return dNdt;
  }
}

data{
  int  n;         // sample size
  int  m;         // number of observations per time-series (without t0)
  real Nstart[n]; // initial values
  real logN[n,m]; // log of observations
  real t0[n];     // starting time
  real time[n,m]; // time of observations
  real tempExp[n];// Arrhenius temperature experimental
}

transformed data { // for the Stan function integrate_ode(), not used here
  real x_r[0];
  int x_i[0];
}

parameters { // see manuscript for full parameter definition
  real r;  // ln of normalization constant for growth rate r
  real K;  // ln of normalization constant for carrying capacity K
  real Er; // activation energy of r
  real EK; // activation energy of K
  real<lower=0> sdev;
}

model {
  // intermediate parameters for handling the stan function integrate_ode()
  real p[2];      // input parameters for ODE
  real N0[1];     // initial value, needs to be a vector for stan. dim =  #(equations in ODE)
  real Nsim[m,1]; // output values, needs to be a matrix for stan. dim1 = #(observations), dim2 =
#(equations in ODE)

  // priors (uninformative)
  r ~ normal(0, 100);
  K ~ normal(0, 100);
  Er ~ normal(0, 100);
  EK ~ normal(0, 100);
  sdev ~ uniform(0, 1000);

// likelihood
  for (i in 1:n){
    p[1] <- exp(r+Er*tempExp[i]); // growth rate
    p[2] <- exp(K+EK*tempExp[i]); // carrying capacity
    N0[1]<- Nstart[i];
    Nsim <- integrate_ode(frmodelode,N0,t0[i],time[i],p,x_r,x_i);
    for (j in 1:m){
      logN[i,j] ~ normal(log(Nsim[j,1]),sdev);
    }
  }
}
```

// Stan model code for Crowley-Martin type 3 ODE:
"Temperature adaptation of predator interference"; K.E. Fussmann, B. Rosenbaum, B.C. Rall; 2016

```
functions{
  // ODE right hand side for Crowley-Martin type 3 functional response
  real[] frmodel_treatment(real t, real[] N, real[] p, real[] x_r, int[] x_i){
    real dNdt[1];
    real bN2;
    bN2 <- p[3]*N[1]*N[1];
    dNdt[1] <- -( bN2 / (1.0 + p[4]*bN2 + p[6]*(p[5]-50.0) + p[4]*bN2*p[6]*(p[5]-50.0) ) ) * p[5] +
p[1]*N[1]*log(p[2]/N[1]);
    return dNdt;
  }
}

data{
  int  n;         // sample size
  int  m;         // number of observations per time-series (without t0)
  real Nstart[n]; // initial values
  real Pstart[n]; // predator density
  real logN[n,m]; // log of observations
  real t0[n];     // starting time
  real time[n,m]; // time of observations
  real tempExp[n];   // Arrhenius temperature experimental
  real tempAdapt[n]; // Arrhenius temperature adaptation
}

transformed data { // for the Stan function integrate_ode(), not used here
  real x_r[0];
  int x_i[0];
}

parameters { // see manuscript for full parameter definition
  real a; // ln of normalization constant for attack coefficient b
  real Ea;
  real Aa;
  real Ia;
  real h; // ln of normalization constant for handling time
  real Eh;
  real Ah;
  real Ih;
  real c; // ln of normalization constant for interference coefficient
  real Ec;
  real Ac;
  real Ic;
  real<lower=0> sdev;
}

model {
  // intermediate parameters for handling the stan function integrate_ode()
  real p[6];      // input parameters for ODE
  real N0[1];     // initial value, needs to be a vector for stan. dim =  #(equations in ODE)
  real Nsim[m,1]; // output values, needs to be a matrix for stan. dim1 = #(observations), dim2 =
#(equations in ODE)

  // priors (uninformative)
  a ~ normal(0, 100);
  Ea ~ normal(0, 100);
  Aa ~ normal(0, 100);
  Ia ~ normal(0, 100);
  h ~ normal(0, 100);
  Eh ~ normal(0, 100);
  Ah ~ normal(0, 100);
  Ih ~ normal(0, 100);
  c ~ normal(0, 100);
  Ec ~ normal(0, 100);
  Ac ~ normal(0, 100);
  Ic ~ normal(0, 100);
  sdev ~ uniform(0, 1000);

  // likelihood
  for (i in 1:n){
    p[1] <- exp( -8.04744 + 0.70394*tempExp[i] ); // growth rate, values from control fitting
    p[2] <- exp( 12.47741 - 0.28329*tempExp[i] ); // carrying capacity, values from control fitting
    p[3] <- exp( a + Ea*tempExp[i] + Aa*tempAdapt[i] + Ia*tempExp[i]*tempAdapt[i] ); // attack
coefficient
    p[4] <- exp( h + Eh*tempExp[i] + Ah*tempAdapt[i] + Ih*tempExp[i]*tempAdapt[i] ); // handling
time
    p[5] <- Pstart[i]; // predator density
    p[6] <- exp( c + Ec*tempExp[i] + Ac*tempAdapt[i] + Ic*tempExp[i]*tempAdapt[i] ); //
interference coefficient
    N0[1]<- Nstart[i]; // hand over scalar initial density to vector
    Nsim <- integrate_ode(frmodel_treatment,N0,t0[i],time[i],p,x_r,x_i);
```

```
    // connect model result to data logN for likelihood
    for (j in 1:m){
      logN[i,j] ~ normal(log(Nsim[j,1]),sdev);
    }
  }
}

generated quantities { // for model comparison only. repeat the steps of the model block and save
log-likelihood value, see loo package
  real p[6];
  real N0[1];
  real Nsim[m,1];
  vector[n*m] log_lik; // log likelihood values for model testing

  for (i in 1:n){
    p[1] <- exp( -8.04744 + 0.70394*tempExp[i] );
    p[2] <- exp( 12.47741 - 0.28329*tempExp[i] );
    p[3] <- exp( a + Ea*tempExp[i] + Aa*tempAdapt[i] + Ia*tempExp[i]*tempAdapt[i] );
    p[4] <- exp( h + Eh*tempExp[i] + Ah*tempAdapt[i] + Ih*tempExp[i]*tempAdapt[i] );
    p[5] <- Pstart[i];
    p[6] <- exp( c + Ec*tempExp[i] + Ac*tempAdapt[i] + Ic*tempExp[i]*tempAdapt[i] );
    N0[1]<- Nstart[i];
    Nsim <- integrate_ode(frmodel_treatment,N0,t0[i],time[i],p,x_r,x_i);

    // compute normal_log value for log-likelihood of lognormal distribution
    for (j in 1:m){
      log_lik[(i-1)*m+j] <- normal_log(logN[i,j], log(Nsim[j,1]), sdev);
    }
  }
}
```

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אני אוהבת אותך מאוד מאוד! אתה החיים, מישפחה ועדר שלי

Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Arbeit selbstständig angefertigt, keine unerlaubten Hilfsmittel verwendet und bisher noch keinen Promotionsversuch unternommen habe.

Katarina Fussmann

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PUBLICATIONS AND CONFERENCE CONTRIBUTIONS

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WORK EXPERIENCE AND INTERNSHIPS

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Roehampton University, London, United Kingdom
Work included field trips to different freshwater streams across England, microscopic analysis of life protist samples, flow cytometry of bacteria, algae and diatoms and the protocol development for biofilm analysis in freshwater sediments. Further, the operation of unisense oxygen optodes to analyse respiration and photosynthesis in freshwater microorganisms

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Work included regular field trips to 8 different groundwater boreholes in Berkshire and Dorset, analysis of bacterial samples with a flow cytometer and microscope samples of protozoan and arthropods. Also, general lab maintenance and ordering required chemicals and equipment via the university booking system

02/2010 - 12/2011 — **Library assistant**
Technische Universität Darmstadt, Germany
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listing and scanning of new books and updating the library database

03/2009 - 12/2009 — **Student assistant in the working group for animal ecology**
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worked on functional response experiments
assisted complex ecological micro- and mesocosm experiments with decomposer organisms of the soil

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